Exotic Annual Grasses in Western Rangelands: Predicting Resistance and Resilience of Native Ecosystems to Invasion

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14. ABSTRACT

Bromus tectorum (hereafter referred to as Bromus) is a non-native annual grass from the Mediterranean region that arrived in the United States in the late 19th century and soon spread throughout the western states. Bromus now dominates millions of hectares of low and midelevation landscapes. Where this occurs, native plant and animal diversity is reduced and sometimes extirpated, fire frequencies are increased, community productivity is decreased, and soil biota and nutrient cycles are altered. This has led to a many research efforts to understand the impact of Bromus on native ecosystems and to identify ways to prevent invasion and/or to restore invaded landscapes.

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Executive Summary

Bromus tectorum (hereafter referred to as *Bromus*) is a non-native annual grass from the Mediterranean region that arrived in the United States in the late 19th century and soon spread throughout the western states. *Bromus* now dominates millions of hectares of low and mid-elevation landscapes. Where this occurs, native plant and animal diversity is reduced and sometimes extirpated, fire frequencies are increased, community productivity is decreased, and soil biota and nutrient cycles are altered. This has led to a many research efforts to understand the impact of *Bromus* on native ecosystems and to identify ways to prevent invasion and/or to restore invaded landscapes.

Unfortunately, almost all efforts to contain or eliminate *Bromus* have been unsuccessful. Therefore, attention has turned to ways that Bromus invasions might be avoided or how invaded areas might be restored. Part of this effort involves understanding what factors promote, and what factors prevent, invasion. Many people believe that invasion by *Bromus* requires disturbance, whether this be churning of the soil surface (as occurs with livestock and off-road vehicles) or fire. However, there are some instances of *Bromus* invading areas long after surface disturbances ceased. A recent (1994) *Bromus* invasion occurred in Canyonlands National Park in a remote, never-grazed grassland with very little human visitation. The invasion occurred in small (<100 m diameter) and distinct patches, indicating that at least in this locality, invasion was controlled by soils or microhabitat characteristics. Upon closer examination, it was observed that the invasion occurred in soil patches dominated by the C_4 perennial grass *Hilaria jamesii*, whereas *Bromus* was unable to invade soils dominated by *Stipa hymenoides* and *S. comata*. This led to a concerted effort to explore the following questions:

1) How can we accurately assess soil characteristics that may have influenced the *Bromus* invasion?
2) What site factors confer resistance to invasion by *Bromus*? Is it soil chemistry, microhabitat, or less herbivory? Can these factors also predict areas susceptible to invasion by *Bromus* and other exotic annual grasses on a landscape and regional scale?
3) Can soil factors that confer resistance be used to suppress *Bromus* while not affecting the germination or success of native plants?
4) Once *Bromus* invades, how does it affect native communities and soil nutrient cycles in the absence of other disturbances? Do these alterations affect the ability of the site to support natives?

These questions are addressed in the following report, with each section addressing each of the above questions.

Section I: How can we accurately assess soil characteristics that may have influenced the *Bromus* invasion?

Four methods of measuring nutrients were compared. Three methods involved using ion-exchange capsules that were charged with different counterion combinations (HCl, HOH, and $NaHCO_3$), and the fourth was conventional chemical extraction. The four methods were not comparable with respect to any nutrient in the five sandy calcareous soils tested. Of the counterion combinations, HCl-resins yielded the most net ion exchange with all measured nutrients except Na^+, NH_4^+, and HPO_4^{2-}, which desorbed in the greatest quantities from HOH-resins. Acidification of the resin environment by H^+ is considered to be the primary mechanism for high nutrient sorption on H^+-containing resins, and greater resin affinity for Cl^- than OH^- the reason for higher HPO_4^{2-} sorption on HOH-resins. Chemical NH_4OAc extractions generally yielded high proportional Ca^{2+}, K^+, and Na^+, an effect that may be attributable to higher soil exchange site affinity for NH_4^+ than for Na^+ or H^+. It is also possible that proportional Ca^{2+} was higher due to dissolution of fine $CaCO_3$ particles by NH_4OAc extraction. Therefore, for studies in calcareous soils we suggest that a nutrient extraction technique that greatly alters soil carbonates through dissolution or precipitation could compromise the accurate measurement of plant-available nutrients.

We then assessed ways to measure 12 nutrients in three sandy soils using resin bags, resin capsules, resin strips (all charged in the same way), and conventional chemical extraction methods. We found that none of these methods gave comparable results. In addition, extraction temperatures also affected results. We suggest that these differences are at least partially due to 1) the different methods extracting nutrients from different volumes of soil and 2) chemical extraction methods dissolving carbonates in the soil, resulting in artificially high calcium numbers. Therefore, before embarking on a study, we suggest it is important to identify the nutrients of foremost interest and to understand their resin sorption dynamics to determine the most appropriate extraction method.

Lastly, we compared the consistency of nutrient extraction among repeated cycles of ion-exchange resin membrane use. We tested two sandy calcareous soils and different equilibration temperatures. No single nutrient retained consistent values from cycle to cycle in all treatments, although both soil source and temperature conferred some influence. We conclude that the most conservative use of resin membranes is single-use.

Bullet Summary of Section I:

- Methods need to be chosen based on the elements of interest, the question being asked, and whether results are to be compared to results of other studies
- Results from one method are not comparable to results using different methods
- Methods should be tested with the soils in question before experimentation is begun.

Section II: What site factors confer resistance to invasion by *Bromus*? Is it soil chemistry, microhabitat, or less herbivory? Can these factors also predict areas susceptible to invasion by *Bromus* and other exotic annual grasses on a landscape and regional scale?

Several factors can determine the success of vascular plants. These include microhabitat conditions, herbivory, and soil chemistry. Microhabitat can alter plant germination, growth, and survival by modifying light, water, nutrients and herbivore damage. Herbivory can directly

impact plant success, and soil chemistry can determine plant performance. Soil chemistry may determine invasion patterns. In Canyonlands National Park, the annual invasive grass *Bromus* generally occurs in areas dominated by *Hilaria* and rarely in areas dominated by *Stipa*. To determine if the success of *Bromus* in *Hilaria* patches was determined by the microhabitat created by *Hilaria*, we examined the effects of plant canopy, plant litter and herbivory on the emergence, growth and survival of *Bromus*. In a field experiment we planted *Bromus* either under the canopy of *Hilaria* or *Stipa* or in the interspace, with and without *Hilaria* litter, and with and without rodent herbivory. We also reciprocally transplanted soils, moving soils from a *Stipa*-dominated area into a *Hilaria* area and vice versa so that soils varied but microhabitats did not. These experiments were conducted in an extreme drought year and an almost average year. *Bromus* emergence and biomass was similar in *Hilaria*-dominated and *Stipa*-dominated sites for all treatments. Being under a plant canopy increased emergence in the drought year, but did not affect emergence in the almost average year. In contrast, plant canopy had negative effects on biomass and survival of *Bromus*. Herbivory negatively affected emergence only in the drought year but had no effect on biomass and decreased survival in both years. *Hilaria* litter increased *Bromus* emergence, did not affect biomass, and decreased survival. Our results support other studies that show facilitative and competitive interactions may change throughout a plant's life cycle and depend on abiotic conditions. Although we found several microhabitat factors to influence *Bromus*, these factors did not differ between patches of *Hilaria* and *Stipa*. This suggests that although these factors influenced *Bromus* success, they did not explain the observed association between *Bromus* and *Hilaria*. We suggest this supports our previous contention that *Bromus* invasion into *Hilaria* areas is explained by soil chemistry.

Based on our observation that the invasion of annual grass appears controlled by soil chemistry, we investigated the effect of site factors on annual grass cover in 432 sites in the Chihuahuan, Mojave, Colorado Plateau, and Great Basin deserts. At these sites, we assessed plant cover, ground cover, slope, aspect, elevation, and soil chemistry. Our results show that soil chemistry defines the difference between uninvaded and invaded patches in most instances. Invaded patches in regions with lower winter precipitation had higher available phosphorus than uninvaded patches. As winter precipitation increased, the importance of phosphorus declined and the importance of available potassium increased. Soil depth was important in areas with shallow soils, and texture played a role in some cases. Because soil texture and nutrients are mappable, annual plant invasions should also be mappable. Site factors that confer resistance to invasion can also be used to design soil amendments to suppress annual grass invasions.

Bullet Summary of Section II

- Resistance to invasion was not determined by microhabitat or herbivory, but soil chemistry at a local scale.
- In deserts with low winter precipitation and high temperatures, and in deserts at higher elevations, phosphorus availability was most important in predicting annual grass cover. In deserts with higher winter precipitation and cooler temperatures, K availability was most important, with P and N availability being of secondary importance. Soil depth can also play a role in areas with very shallow soils.
- Because soil chemistry is mappable, resistance to invasion is also mappable. Factors operative at a local scale are applicable at a regional scale unless environmental conditions are very different. However, controls on annual grass appear different from region to region.

Section III: Can soil factors that confer resistance be used to suppress *Bromus* while not affecting the germination or success of native plants?

The objective of this part of the project was to identify soil additives that allowed germination but inhibited emergence of *Bromus tectorum*, while not affecting germination or emergence of the native perennial grass *Hilaria jamesii*. Based on data from previous studies that Bromus was stimulated by soil nitrogen (N), phosphorus (P), and /or potassium (K), we focused on altering these nutrients. Most water-soluble treatments we added inhibited *Bromus* germination and/or emergence. We attribute the inhibitory effects of these treatments to excessive salinity and ion-specific effects of the additives themselves. An exception to this was oxalic acid, which showed no effect on *Bromus*. Most water-insoluble treatments had no effect in soils with high P, but did have an effect in soils with low P. Zeolite was effective regardless of P level, probably due to the high amounts of Na^+ it added to the soil solution. Most treatments at higher concentrations resulted in lower *Bromus* emergence rates when added to soils currently dominated by *Bromus* than when added to soils from uninvaded (but theoretically invadable) *Hilaria* soils. This difference is possibly attributable to inherent differences in labile soil P.

In *Stipa* soils, considered uninvadable by *Bromus*, additions of high amounts of N resulted in lower emergence. This may have been an effect of NH_4^+ interference with uptake of K and/or other cations, or toxicity of high N. We also saw a positive relationship between *Bromus* emergence and pH in *Stipa* soils. *Hilaria* development parameters were not as susceptible to the treatments, regardless of concentration, as *Bromus*. Our results suggest that there are additions that may be effective management tools to inhibit *Bromus* in calcareous soils, including 1) high salt applications, 2) K-reducing additions (e.g., Mg), and/or 3) P-reducing additions .

We then grew *Bromus* and *Hilaria* alone and together in each of nine soil treatments that manipulated levels of soil phosphorus and potassium. *Hilaria* showed no biomass decline with any of the applied treatments when grown in monoculture or in combination with *Bromus*. However, *Hilaria* biomass in the combination pots was reduced by 50% or more relative to the monoculture pots. In contrast to *Hilaria*, most treatments (except CaO) reduced *Bromus* biomass when grown in monoculture. However, in the combination pots, the presence of *Hilaria* in the pots with *Bromus* ameliorated the negative effect of the treatments and *Bromus* biomass showed no declines with our amendments. In fact, *Bromus* biomass was enhanced by up to 400% when grown with *Hilaria*, indicating that the presence of the native grass facilitated growth in *Bromus*. This may be explained by root CEC: as expected when comparing an annual with a perennial grass, *Bromus* had much higher root CEC than *Hilaria* and *Bromus* tissue concentrations for all elements were higher in *Hilaria* except for Na and Mn. All treatments except CaO (the treatment that did not suppress *Bromus* biomass) increased Na uptake in *Bromus*. However, tissue Na in *Bromus* was always lower than that of *Hilaria*, indicating *Bromus* is better able to discriminate against this element. Combined with findings from other studies, we hypothesize that *Bromus* is more negatively impacted by high soil salt levels than *Hilaria*.

We also speculate that the observed facilitation of *Bromus* by *Hilaria* and the suppression of *Hilaria* by *Bromus* is likely a result of either 1) *Bromus* tapping into *Hilaria's* mycorrhizal network, thus gaining access to water and nutrients that *Hilaria* would otherwise receive or 2) *Hilaria* roots exuding compounds that benefit *Bromus*. This would also include water and dissolved nutrients made available by hydraulic redistribution of *Hilaria*. Because *Bromus* roots

have a much higher CEC relative to *Hilaria* roots, *Bromus* would likely be able to outcompete *Hilaria* for any nutrients released into the soil. In summary, land managers are unlikely to ever extirpate *Bromus*. Adding high levels of salt to the soils when restoring areas may assist native reestablishment by temporarily suppressing *Bromus*. However, the presence of natives is likely to favor the continued presence of *Bromus* by facilitating *Bromus* growth.

Results from these laboratory experiments were then used to design field experiments. First, we conducted a reciprocal soil transplant experiment to determine whether microhabitat or soil chemistry explained the observed pattern of *Bromus* in *Hilaria*-dominated areas. Emergence and biomass of *Bromus* was similar regardless of whether soil was in the *Hilaria* or *Stipa* sites; however, emergence was higher in soils that originated in *Hilaria* sites suggesting that soil chemistry explains *Bromus* invasion patterns.

Second, we investigated soil amendments that had been successful in the laboratory at allowing *Bromus* germination but reducing emergence without having negative effects on *Hilaria*. We conducted experiments in two different years where we applied four amendments ($CaCl_2$, $MgCl_2$, NaCl and zeolite) at various concentrations to reduce available P and K. No amendments negatively affected *Hilaria* biomass, but NaCl slightly reduced emergence. All amendments except 4x $CaCl_2$ and 0.5x zeolite negatively affected *Bromus* emergence and/or biomass; however, amendments did not always affect emergence and biomass similarly. In addition, amendment effectiveness depended on amendment concentration, year of application, and in some cases, the effects of amendments changed over time where emergence and/or biomass were first depressed and then there was no effect or a stimulatory effect. Zeolite (1x) had the strongest negative effect on *Bromus* with little effect on *Hilaria*. In a laboratory experiment, zeolite significantly increased Zn, Fe, Mn, Cu, exchangeable Mg, exchangeable K, exchangeable Na and NH_4 while decreasing Ca in the soil. Our results reveal several possible amendments to control *Bromus.* However, these same amendments can stimulate emergence and/or biomass in later years. Variability in effectiveness due to abiotic factors such as precipitation and soil type must be accounted for when establishing management plans.

Bullet Summary of Section III

- There are soil amendments that successfully suppress *Bromus* yet have little effect native plants. These additives exploit the fact that *Bromus* appears salt-sensitive whereas native grasses are salt-tolerant.
- However, there is evidence that the effect of the tested amendments in the field change with precipitation regimes and over time and amendments that suppressed *Bromus* in one year can actually stimulate it the next year. Therefore, before any of these amendments are used, long-term experiments are needed.
- The presence of natives stimulates the growth of *Bromus*. Thus it is unlikely we will ever extirpate Bromus from US rangelands. Instead, we need to focus on assisting native plant establishment and continued success within invaded sites.

Section IV: Once *Bromus* invades, how does it affect native communities and soil nutrient cycles in the absence of other disturbances? Do these alterations affect the ability of the site to support natives?

Biological soil crusts: Biological soil crusts are an essential part of desert ecosystems

throughout the world, as they are important in soil stabilization and soil fertility. They are dominated by mosses and lichens, are the main source of nitrogen for Colorado Plateau ecosystems. Previously it was thought that these communities showed little change from year to year. However, after seven years of monitoring, we have found the cover of mosses and lichens can increase dramatically over short time periods, often going from just above 0% cover to as high as 9% cover in only six months. During our study time, cover of the nitrogen-fixing lichen *Collema* declined throughout the study, going from 19% in 1996 to as low as 2% in 2003 in response to a large increase in both maximum and minimum temperatures during the study period. Changes in chlorolichen cover (lichens with green algal phycobionts that cannot fix nitrogen), on the other hand, appeared to be driven by precipitation. *Bromus* invasion did not affect species richness in never-grazed plots, but a 50-year invasion reduced species richness in intermittently-grazed plots. The recent Bromus invasion did not affect cover for most species. However, *Bromus* did accelerate the decline in cover of *Collema*. Extended drought resulted in a large decline of all species in 2003. Loss of lichen and moss cover is expected to affect many aspects of this ecosystem. Of special concern is the loss of *Collema*, as it is the dominant source of nitrogen for this ecosystem.

Vascular plants: We also monitored the effect of *Bromus* on two native grass communities (one dominated by the C_4 grass *Hilaria* and the other dominated by the C_3 *Stipa*) for seven years (1996-2003). Grass cover in both communities has been declining since 1996 due to climatic conditions in both the invaded and uninvaded plots. The presence of *Bromus* has not accelerated or slowed this decline. When species lists and richness in the invaded areas are compared to species lists from 1967 and lists from the uninvaded plots, there has been no change in species present. Therefore, we conclude that the presence of *Bromus* has not affected these native plant communities in the absence of grazing and fire.

Soil phosphorus: Phosphorus (P) is a plant-essential nutrient that is often limiting in the high pH soils found in deserts as it complexes with calcium carbonate and becomes unavailable to plants. Unfortunately, little is known about conditions that free up the unavailable P. In our first set of field measurement, we showed that plant available P changes on a monthly basis. During wet years, available P is higher in the winter at sites with *Bromus*. However, there is no difference during dry years. We showed that recalcitrant P has a pronounced annual cycle as well. This was surprising, as this P fraction is considered stable and hence unlikely to increase or decrease in short time periods.

In a second set of field studies, we followed P dynamics following a new *Bromus* invasion. We found that in uninvaded soils dominated by *Hilaria*, there is a weak seasonal pattern of plant available P cycling. In contrast, P in soils dominated by *Stipa* showed very little change through the year. Interestingly, when either species was invaded by *Bromus*, the amplitude of the positive side of the cycle increases, but there was never less plant available P than when the native species grows alone. In other word, *Bromus* increased plant available P in some seasons (winter), but available P never went below the native species levels. The severe drought in 2003 dampened the P cycle considerably for both species and for the *Bromus*/native species mix.

Using controlled conditions in the greenhouse, we tested for the effect of *Bromus* on soil P fractions. Surprisingly, plant available P increased when Bromus is grown in the soil, regardless of the soil type. In addition we found enormous changes in the recalcitrant P with the presence of *Bromus*, suggesting that *Bromus* is able to free up and utilize fractions of P long

considered unavailable to vascular plants.

Soil nitrogen: We measured plant-available nitrogen (N) and plant and soil isotopic composition in soils dominated by *Hilaria* and *Stipa*, with and without *Bromus*. The *Bromus* invasion has significantly altered soil N cycling processes in both native grassland communities. A long-term incubation experiment was conducted to determine the mechanisms for these observed changes. The results of this experiment suggest that different processes are occurring in *Stipa* and *Hilaria* communities that are leading to the same effects as measured by plant-available N availability and stable isotope composition. In *Stipa* communities there is an increase in the amount of labile soil organic N with *Bromus* invasion, coupled with an overall increase in microbial N cycling as measured by both gross and net rates of soil N transformations (mineralization, immobilization, and nitrification). For *Hilaria* communities there was no effect of *Bromus* invasion on labile soil N pools, but as with *Stipa* communities, overall N cycling rates were greater as measured by gross N fluxes. In addition, differences in the stable isotopic composition ($\delta^{13}C$) of *Hilaria* (C_4) and *Bromus* (C_3) allow for the partitioning of microbial utilization between these two substrates.

It was observed that *Bromus* invasion appears to stimulate the activity of at least a portion of the soil bacterial pool, which preferentially decomposes *Bromus* litter rather than *Hilaria* litter. Analyses of soil microbial community structure also indicate that *Bromus* invasion significantly decreases the proportion of fungi in both native communities. This suggests that *Bromus* invasion can significantly alter the composition of the soil microbial community by changing the proportion of soil bacteria to fungi and increasing bacterial activity. These shifts in community structure and substrate utilization lead to increased rates of soil N cycling that in turn affect the amounts of plant-available N in these arid grassland ecosystems. In addition, soil nitrogen isotope may track historical changes following invasion.

Soil food web structure and growth of natives in soils dominated by Bromus *for over 50 years*: The presence of the exotic annual grass *Bromus tectorum* altered soil food webs in areas both recently invaded and those invaded for 50 years are compared to uninvaded areas. Recently invaded soils showed a reduction in both species richness and abundance of soil micro-invertebrates and nematodes, with a more dramatic reduction after 50 years. Although invaded soils showed an increase in active fungal biomass and active/total fungal biomass when compared to uninvaded soils, species richness of fungi declined. The invasion of *Bromus*, combined with previous livestock grazing, also led to decreased plant species richness. However, despite the depauperate soil fauna, decomposition rates were the same in uninvaded and invaded sites and soil nutrient availability (e.g., nitrogen) was sufficiently high to support both native and exotic grasses. When seeds of *Hilaria jamesii* were planted into these three soils (uninvaded, recently invaded, invaded 50 years), germination and survivorship was not affected. Aboveground *Hilaria* biomass was significantly greater in soils dominated by *Bromus* for 5 years than uninvaded soils or those dominated for 50 years. We attributed the *Hilaria* response to differences in soil nutrients, especially nitrogen, phosphorus, and potassium, as these nutrients were elevated in the soils that produced the greatest *Hilaria* biomass. Thus, despite the fact that *Bromus* significantly altered soil food webs, this did not affect measured soil processes or preclude successful establishment and growth of the native grass *Hilaria*. This suggests that it is not soil species richness *per se* that determines soil process rates or plant success, but that instead that the presence of a few critical species can keep the ecosystem function high. However, as the presence of *Bromus* reduces key soil nutrients over time, native plant success

may be eventually suppressed.

Bullet Summary of Section IV

- In the absence of grazing and fire, *Bromus* did not negatively affect vascular plant communities. Therefore, restoration of invaded grasslands appears to be a reachable management goal, but may require restriction of other disturbances.
- *Bromus* did not affect most lichen and moss species. However, it accelerated the decline in cover of the dominant lichen *Collema*. Because *Collema* is the major source of nitrogen for this ecosystem, this is of great concern. Therefore, restoration efforts should include inoculation of this lichen.
- *Bromus* altered soil P. However, changes in soil P appear to be seasonal (winter) and only during wet years.
- *Bromus* increased N availability in the lightly-invaded *Stipa* communities but not in the heavily-invaded *Hilaria* communities. Therefore, these changes are unlikely to favor *Bromus* over natives. However, increased N cycling rates will likely decrease soil N over time
- *Bromus* dramatically altered both the abundance and species composition of soil food webs. Site alterations by *Bromus* did not affect the ability of these soils to support growth of the native grass *Hilaria* that once dominated invaded sites. Therefore, managers likely do not need to manipulate soil food webs to successfully restore invaded areas.

Conclusions and Future Research Directions

During this project, we have learned a great deal about the characteristics of exotic annual grasses in general, and *Bromus tectorum* in specific. We have determined that soil chemistry plays a major role in determining whether or not a site will be invaded, and that other site characteristics (e.g., microhabitat, herbivory) are not as important. We determined that the availability of phosphorus and potassium is the most important elements to consider in desert environments. Because soil chemistry is mappable, resistance to invasion is also mappable. Factors operative at a local scale are applicable at a regional scale unless environmental conditions are very different (e.g., very low to high elevations). However, controls on annual grass differ among regions. This correlative study needs to be followed up with experimental manipulations to determine the mechanisms behind the observed patterns.

Based on the influence of soil chemistry on annual grass invasion, we also investigated soil amendments that can successfully suppress *Bromus* yet have little effect on native plants. We found *Bromus* to be very salt-sensitive whereas native grasses are salt-tolerant and, thus, Bromus could be suppressed with the simple addition of NaCl (table salt). However, there is evidence that the effect of the tested amendments in the field change with precipitation regimes and over time and amendments that suppressed *Bromus* in one year can actually stimulate it the next year. Therefore, before any of these amendments are used, long-term experiments are needed.

The presence of native plants stimulates *Bromus* growth. We need to understand the mechanisms behind this observation, as this will impact any restoration effort.

Once *Bromus* invades, it has differential effects on the native communities, depending on what species are present prior to the invasion. In the absence of grazing and fire, *Bromus* did affect vascular plant communities. Therefore, restoration of invaded grasslands appears to be a

reachable management goal, but may require restriction of other disturbances. However, *Bromus* did accelerate the decline in cover of the dominant lichen *Collema*. Because *Collema* is the major source of nitrogen for this ecosystem, this is of great concern. Therefore, restoration efforts should include inoculation of this lichen. Ways to enhance restoration of this lichen need to be explored.

Bromus was also shown to alter soil P. However, changes in soil P appear to be seasonal (winter) and only during wet years. Changes in N availability appeared minor in the heavily-invaded *Hilaria* communities. Therefore, these changes are unlikely to favor *Bromus* over natives during restoration efforts. However, increased N cycling rates will likely decrease soil N over long time periods (>100 years). Although *Bromus* alters nutrients slightly, it dramatically alters both the abundance and species composition of soil food webs. However, site alterations by *Bromus* do not affect the ability of these soils to support growth of the native grass *Hilaria* that once dominated these soils. Therefore, managers likely do not need to manipulate soil food webs or soil chemistry to successfully restore invaded areas.

Section I: How can we accurately assess soil characteristics that may have influenced the *Bromus* invasion?

Four methods of measuring nutrients were compared. Three methods involved using ion-exchange capsules that were charged with different counterion combinations (HCl, HOH, and $NaHCO_3$), and the fourth was conventional chemical extraction. The four methods were not comparable with respect to any nutrient in the five sandy calcareous soils tested. Of the counterion combinations, HCl-resins yielded the most net ion exchange with all measured nutrients except Na^+, NH_4^+, and HPO_4^{2-}, which desorbed in the greatest quantities from HOH-resins. Acidification of the resin environment by H^+ is considered to be the primary mechanism for high nutrient sorption on H^+-containing resins, and greater resin affinity for Cl^- than OH^- the reason for higher HPO_4^{2-} sorption on HOH-resins. Chemical NH_4OAc extractions generally yielded high proportional Ca^{2+}, K^+, and Na^+, an effect that may be attributable to higher soil exchange site affinity for NH_4^+ than for Na^+ or H^+. It is also possible that proportional Ca^{2+} was higher due to dissolution of fine $CaCO_3$ particles by NH_4OAc extraction. Therefore, for studies in calcareous soils we suggest that a nutrient extraction technique that greatly alters soil carbonates through dissolution or precipitation could compromise the accurate measurement of plant-available nutrients.

We then assessed ways to measure 12 nutrients in three sandy soils using resin bags, resin capsules, resin membranes (all charged in the same way), and conventional chemical extraction methods. We found that none of these methods gave comparable results. In addition, extraction temperatures also affected results. We suggest that these differences are at least partially due to 1) the different methods extracting nutrients from different volumes of soil and 2) chemical extraction methods dissolving carbonates in the soil, resulting in artificially high calcium numbers. Therefore, before embarking on a study, we suggest it is important to identify the nutrients of foremost interest and to understand their resin sorption dynamics to determine the most appropriate extraction method.

Lastly, we compared the consistency of nutrient extraction among repeated cycles of ion-exchange resin membrane use. We tested two sandy calcareous soils and different equilibration temperatures. No single nutrient retained consistent values from cycle to cycle in all treatments, although both soil source and temperature conferred some influence. We conclude that the most conservative use of resin membranes is single-use.

How can we accurately assess soil characteristics that may have influenced the *Bromus* invasion?

- Methods need to be chosen based on the elements of interest, the question being asked, and whether results are to be compared to results of other studies
- Results from one method are not comparable to results using different methods
- Methods should be tested with the soils in question before experimentation is begun.

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COMPARISON OF METHODS FOR NUTRIENT MEASUREMENT IN CALCAREOUS SOILS: ION-EXCHANGE RESIN BAG, CAPSULE, MEMBRANE, AND CHEMICAL EXTRACTIONS

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Four methods for measuring quantities of 12 plant-available nutrients were compared using three sandy soils in a series of three experiments. Three of the methods use different ion-exchange resin forms—bags, capsules, and membranes—and the fourth was conventional chemical extraction. The first experiment compared nutrient extraction data from a medium of sand saturated with a nutrient solution. The second and third experiments used Nakai and Sheppard series soils from Canyonlands National Park, which are relatively high in soil carbonates. The second experiment compared nutrient extraction data provided by the four methods from soils equilibrated at two temperatures, "warm" and "cold." The third experiment extracted nutrients from the same soils in a field equilibration. Our results show that the four extraction techniques are not comparable. This conclusion is due to differences among the methods in the net quantities of nutrients extracted from equivalent soil volumes, in the proportional representation of nutrients within similar soils and treatments, in the measurement of nutrients that were added in known quantities, and even in the order of nutrients ranked by net abundance. We attribute the disparities in nutrient measurement among the different resin forms to interacting effects of the inherent differences in resin exchange capacity, differences among nutrients in their resin affinities, and possibly the relatively short equilibration time for laboratory trials. One constraint for measuring carbonate-related nutrients in high-carbonate soils is the conventional ammonium acetate extraction method, which we suspect of dissolving fine $CaCO_3$ particles that are more abundant in Nakai series soils, resulting in erroneously high Ca^{2+} estimates. For study of plant-available nutrients, it is important to identify the nutrients of foremost interest and understand differences in their resin sorption dynamics to determine the most appropriate extraction method. (Soil Science 2002;167:666–679)

Key words: Soil nutrient extraction, ion-exchange resin bags, capsules, membranes, chemical extraction, calcareous soils.

MEASURING plant-available soil nutrients with sensitivity to spatial and temporal variation in soil properties and other environmental conditions is an ongoing challenge for soil researchers. Nutrient bioavailability is a function of soil chemical, physical, and mineralogical properties that govern exchange reactions (Cooperband and Logan 1994; Dobermann et al., 1994), nutrient concentration, diffusion (Skogley et al., 1990; Abrams and Jarrell 1992; Skogley and Dobermann 1996), and biogeochemical processes such as mineralization. These factors are further affected by environmental conditions such as soil moisture and temperature (Binkley 1984; Skogley and Schaff 1985; Yang et al., 1991b).

Chemical extractions are conventional for measuring nutrient availability, but ion-exchange

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resins, demonstrated to be effective measures of soil nutrients in both terrestrial and aquatic ecosystems (Yang et al., 1991a; Abrams and Jarrell 1992; Dobermann et al., 1994), may be preferable in some studies (see Skogley and Dobermann, 1996 for review). Chemical extraction provides a static measure of potential nutrient supply (Gibson et al., 1985), in contrast to resins which, as ionic exchangers, represent an integration of bioavailable nutrient dynamics over a specified incubation period (Christensen and Posner 1980; Cooperband and Logan 1994; Skogley and Dobermann, 1996). In addition, resins are sensitive to environmental conditions (Binkley and Matson, 1983; Skogley, 1992), more efficient for measuring multiple soil nutrients than an equal number of chemical extractions (Schoenau et al., 1993), inexpensive, and nondestructive with respect to soil chemistry and mineralogy (Cooperband and Logan, 1994).

Resins have been used to simulate both soil colloids (e.g., Cooperband and Logan 1994; Skogley and Dobermann, 1996) and plant roots (e.g., Yang et al., 1991a and b; Qian et al., 1992). The acidifying effect of resins with desorption of a H^+ countercation is similar to that of plant roots, although whether it occurs in comparable rates and/or quantities is unknown. Also similar to root processes are the effects of cation uptake on that of anions and vice versa, due to charge-balance relations and shifts in soil equilibria (e.g., Yang et al., 1991a; Barber, 1995). The dynamic colloidal effects of resins, however, are very much like that of a soil. Hence, ion-exchange resins embody particular characteristics of both biological and mineral components of soil ecosystems.

Despite the application of ion-exchange resins for over 40 years (Amer et al., 1955) and their general acceptance as a method for detection of soil nutrient levels, methods of resin use are not uniform and the interpretive differences among varying methods are poorly understood. Major differences among different resin forms (resin bags, capsules, and membranes) are exchange capacity (~32.1 mEq of charge per bag compared with 2.2 mEq/capsule and 1.2 mEq/membrane), shape, and the mesh barrier containing the resin beads of bags and capsules. Theoretically, the spherical shape of resin capsules and bags allows for a geometrically consistent reactive surface area (Skogley et al., 1990), whereas the edges of a resin membrane may become saturated with high-affinity ions before the interior area, thereby decreasing the overall exchange rates. However, resin membranes, which are flat, should also maximize contact with the soil matrix (Cooperband and Logan, 1994) and are the only resin method for which the reactive surface area can be accurately calculated; bags and capsules are filled with beads of varying surface area that is estimated. Additionally, the encasing mesh of bags and capsules may impose a diffusion barrier to the internal beads, allowing two different diffusion rates inside and outside of the mesh (Abrams and Jarrell, 1992; Cooperband and Logan 1994). Also, soil particles and fine roots often become embedded in or behind the mesh and are difficult to remove entirely, and can result in questionable results (Saggar et al., 1990).

Our overarching objective was to compare nutrient extraction data from different resin media and conventional chemical extraction techniques to determine which would be most appropriate for field studies. Although many chemical extraction techniques originally were designed for agronomic applications (e.g., Bohn et al., 1979), both resin and chemical approaches are widely used in ecological studies to quantify spatial and temporal variations in nutrient bioavailability. Our chemical methods were ammonium acetate (NH_4OAc), bicarbonate, DTPA, and KCl extraction of 12 plant-available nutrients. We performed these comparisons in three formats. The first was sand saturated with a nutrient solution of known concentrations. The second was a comparison of two different soil series in temperature-controlled environments. The third was a field-based comparison in the same soils that were used in the temperature-controlled experiments.

METHODS

Sand Saturated with Bolds Nutrient Solution

Resin bags were constructed with commercial nylon stockings filled with 8 g bipolar (H^+ and OH^- counterions) ion-exchange resin beads. Bipolar (H^+/OH^-) resin capsules were obtained (WECSA, Fort Collins, CO). Cation-exchange membranes (CEMs) (CR 67, Dynambio, Madison, WI) were cut to 3.5 × 5 cm and charged with H^+ by placing them in 0.2 *M* HCl for 2 h with the solution replaced halfway through the equilibration period. Anion-exchange membranes (AEMs) (AR 204, Dynambio), also 3.5 × 5 cm, were charged with OH^- in the same manner using 0.5 *M* NaOH.

Sand was sterilized in 1-L quantities. The sand was soaked for 5 min in 1.5 L of 1.0% acetic acid and rinsed of acetic acid with deionized (DI) water. Then, the sand was alternately washed and rinsed with 0.5% acetic acid and DI water, and

then rinsed with 2 L of boiling DI water. The sand was then autoclaved and dried in a 150 °C oven.

In 15 clear, acid-washed 9-oz plastic cups, 75 mL nutrient solution (Bold, 1957) was added to 250 g sterilized sand (nutrient quantities added are in Table 1). Sand was chosen to reduce the effects of cation exchange with clay colloids. Five replicates of each of the three resin forms were embedded in the saturated sand. AEMs and CEMs were placed back to back with a plastic membrane between them. Cups were covered with plastic wrap and allowed to equilibrate for 1 week. Ambient temperatures were 12 to 22 °C. At the end of the exchange period, all resins were collected, rinsed with DI water, and placed in a freezer at 0 °C until extraction. At the Soil and Plant Analysis Laboratory at Brigham Young University (SPAL), ions were desorbed from all resins in 2 *M* HCl for 1 h and all except inorganic N were measured by inductively coupled plasma spectrometry. NH_4^+-N and NO_3^--N were extracted by steam distillation in a H_3BO_3 indicator solution with MgO and Devarda alloy, and determined by titration with H_2SO_4 (Keeney and Nelson, 1982). Results were reported in $\mu g\ resin^{-1}$ whether bag, capsule, or membrane, and converted to micromoles of ionic charge per resin ($\mu mol_c\ resin^{-1}$). Five replicates of sand and nutrient solution with no resins were treated in the same manner and measured for NH_4OAc-extractable calcium, potassium, magnesium, and sodium at pH 8.5 (Ca^{2+}, K^+, Mg^{2+}, and Na^+, respectively; Normandin et al., 1998); DTPA-extractable copper, iron, manganese, and zinc (Cu^{2+}, Fe^{2+}, Mn^{2+}, and Zn^{2+}, respectively; Lindsay and Norwell, 1978); KCl-extractable inorganic nitrogen (NH_4^+-N and NO_3^--N); and bicarbonate-extractable phosphorus (HPO_4^{2-}-P; Olsen et al., 1954). Results were reported in ppm and converted to $\mu mol_c\ kg^{-1}$.

Because the actual volume of soil subject to measurement by ion-exchange resins is unknown and the exchange capacity of the three resin forms differs, we converted all data to percentages of total ions of corresponding charge. Proportions were arcsin-transformed and analyzed among the four methods (chemical and three resin extractions) by multivariate analysis of variance (MANOVA). Na^+ was disregarded from the membrane data due to excessively high Na^+ data from initial charging with NaOH. Membrane Na^+ values were therefore estimated based on the mean proportion of Na^+ extracted by resin bags, resin capsules, and chemical methods, among which there were no significant differences in proportional Na^+. In addition, nutrients were ranked according to net abundance as another means of comparison among methods.

Temperature-Controlled Comparison of Resin Forms in Canyonlands Soil

Soils from the Nakai and Sheppard series (Table 2) were collected from two sites within the Needles District of Canyonlands National Park (CNP) in southeast Utah (38.17°N, 109.98°W), an arid ecosystem averaging 11.6 °C and 214 mm annual precipitation (1965–1997; Miller, 2000). The soils were sieved (2 mm) and mixed with enough DI water to make a saturated paste (Rhoades, 1982). Within each soil type, 10 replicates each of resin bags, capsules, and membrane pairs were embedded in the saturated pastes, and cups were covered with plastic wrap. In February 2000, five replicates of each resin type and soil combination (for a total of 30 replicates) were placed in a cold frame at the Denver Botanic Gardens (DBG, Denver, CO) for the cold (average maximum and minimum temperatures for the incubation period were 23 and −4 °C, respectively) treatment. Five of each combination were placed in a seedling propagator room at DBG for the warm (average maximum and minimum temperatures were 34 and 18 °C, respectively) treatment. Samples were equilibrated for 1 week, at the end of which all resin media were removed, rinsed thoroughly with DI water, and stored at 0 °C. Extraction of resins and soils was as described above at SPAL.

Because nitrogen can undergo rapid microbial transformations and accurate Na^+ data were unavailable from resin membranes, NH_4^+-N, NO_3^--N, and Na^+ data were disregarded in calculating nutrient percentages. Data analysis was as described above.

Field Comparison of Resin Forms

On 11 March, 2000, resins were placed in the field at the same sites from which soil was collected for the temperature-controlled experiments (Table 2) (Walkley and Black, 1934; Rhoades, 1982; Day, 1965; Chapman 1965; Allison and Moode, 1965; Normandin et al., 1998; Lindsay and Norwell, 1978; Schoenau and Karamonos, 1993; Bremner, 1996; Olsen et al., 1954). At each site, five replicates each of resin bags, capsules, and membranes were placed in the A horizon at 5- to 7-cm depth. Soil moisture and temperature were recorded at 10-cm soil depth once per hour by climate stations close to the plots.

TABLE 1

Mean, SE, and percent nutrients added to and measured in a sand/nutrient solution*

	Added in solution		Extracted															
			Chemical				Resin bags				Resin capsules				Resin membranes			
Nutrient	μmol_c $sample^{-1}$	%	μmol_c $sample^{-1}$	SE	%		μmol_c bag^{-1}	SE	%		μmol_c $caps.^{-1}$	SE	%		μmol_c $memb.^{-1}$	SE	%	
Ca^{2+}	33.7	6.2	643.0	447	36.4	a	33.3	2.9	12.4	d	29.9	1.2	15.3	c	93.2	6.4	25.8	b
Cu^{2+}	0.9	0.2	1.7	1	0.1	d	2.2	0.1	0.8	b	2.6	0.3	1.4	a	1.6	0.1	0.4	c
Fe^{2+}	2.7	0.5	13.3	4	0.8	c	16.5	1.8	6.2	a	15.1	2.7	7.6	a	16.2	2.2	4.4	b
K^+	197.8	36.7	150.9	96	8.8	d	43.0	0.6	16.2	b	34.5	0.7	17.7	a	53.7	3.7	14.9	c
Mg^{2+}	45.5	8.4	165.3	25	9.6	a	17.1	1.0	6.4	c	13.9	1.0	7.1	b	33.7	2.6	9.3	a
Mn^{2+}	1.1	0.2	2.7	1	0.2	a	0.3	0.03	0.1	b	0.2	0.01	0.1	b	0.6	0.05	0.2	a
Na^+	252.4	46.9	727.3	93	42.7		113.5	2.3	42.7		90.1	4.0	46.2				[43.9]	
NH_4^+			21.1	24	1.3	c	39.9	1.3	15.1	a	8.8	0.8	4.6	b	3.0	0.4	0.9	c
Zn^{2+}	4.6	0.9	2.5	1	0.14	b	0.1	0.01	0.05	d	0.1	0.01	0.07	c	0.9	0.3	0.25	a
NO_3^-	219.9	65.1	9.6	3	20.6	a	3.1	0.4	6.8	c	4.5	0.6	14.8	b	4.5	0.5	14.8	b
HPO_4^{2-}	64.3	19.0	23.8	2	51.0		24.2	0.1	53.3		16.3	0.6	54.3		16.3	1.2	53.3	
SO_4^{2-}	53.7	15.9	13.4	6	28.5	b	18.2	0.6	39.9	a	9.3	0.6	30.9	b	9.8	0.6	32.0	b

*Percentages refer to the proportions of each cation or anion relative to total ions of the same charge. Na^+ data were exceedingly high from membrane data due to initial charging of AEMs with NaOH and were not included in proportional calculations. Because there are no significant differences in relative amounts of Na^+ extracted by the remaining extraction methods, cation percentages for membranes are based on the assumption that Na^+ represented 43.9% of all cations desorbed from membranes (the mean of the other three methods). Different letters indicate significant ($P < 0.05$) differences among extraction methods in arcsin-transformed nutrient proportions.

TABLE 2
Characteristics of two CNP soils used for resin comparisons.*

	Nakai	Sheppard	Nutrient	Nakai series	Sheppard series
USDA subgroup†	Typic Calciorthids	Typic Torripsamments	Exchangeable Ca ($\mu mol_c\ kg^{-1}$)**	131,158	98,270
Bulk density ($g\ cc^{-1}$)†	1.5	1.6	Cu ($\mu mol_c\ kg^{-1}$)Ψ	12.4	31.7
OM (%)‡	1.2	0.3	Fe ($\mu mol_c\ kg^{-1}$)Ψ	66.8	49.3
PH§	8.1	8.1	Available K ($\mu mol_c\ kg^{-1}$)Δ	6331	954
EC ($dS\ M^{-1}$)§	0.9	0.5	Exchangeable K ($\mu mol_c\ kg^{-1}$)	7068	878
% Sand¶	61.6	85.6	Exchangeable Mg ($\mu mol_c\ kg^{-1}$)	14,877	2908
% Silt	26.1	7.1	Mn ($\mu mol_c\ kg^{-1}$)Ψ	168	52.7
% Clay	12.3	7.3	Total N (ppm)∂	868	230
CEC ($cmol_c\ kg^{-1}$)‖	5.9	2.0	Exchangeable Na ($\mu mol_c\ kg^{-1}$)	2806	2964
% $CaCO_3$ equiv.#	10.2	13.5	P ($\mu mol_c\ kg^{-1}$)∞	463	28.3
			SO_4-S ($\mu mol_c\ kg^{-1}$)Ψ	283	140
			Zn ($\mu mol_c\ kg^{-1}$)Ψ	11.5	10.4

*Values are averaged from 6–10 replicates. Single-factor ANOVA showed that all differences in nutrients between soil types are significant ($P < 0.05$) except for Na^+ and Zn^{2+}.
†USDA & SCS 1991; ‡Walkley and Black (1934); §Determined with saturated paste (Rhoades, 1982); ¶Texture was determined by the hydrometer method (Day, 1965); ‖Chapman (1965); #measured by HCl neutralization (Allison and Moode, 1965) and includes any soil constituent that neutralizes acid; **All exchangeable nutrients were extracted with ammonium acetate at pH 8.5 ($NH_4C_2H_3O_2$; Normadin et al., 1998); ΨDTPA extraction (Lindsay and Norwell, 1978); ΔSchoenau and Karamonos (1993); ∂Kjeldahl analysis (Bremmer, 1996); ∞Olsen et al. (1954).

Soil temperature was measured with a Campbell CS615 water content reflectometer. Mean monthly soil temperatures for the March, April, May, and June equilibration periods at the Nakai soils site were 8, 15, 24, and 32 °C, respectively, and soil moisture was 12%, 6%, 4%, and 2% by volume, respectively. Mean monthly soil temperatures for the same periods at the Sheppard soils site were recorded as 10, 18, 24, and 31 °C, and soil moisture was 10%, 7%, 5%, and 3% by volume, respectively. Overall soil temperature and moisture means for the Nakai and Sheppard soils were 19.0 and 20.0 °C, and 6.4% and 6.6%, respectively. Precipitation events on 20 March, 27 March, and 7 May resulted in detectable but transient increases in soil moisture.

Resins were collected 94 days later on 13 June 2000. Nutrients were extracted at SPAL and data were analyzed as described above. Unless stated otherwise, all significance refers to $P < 0.05$.

RESULTS

Sand Saturated with Bold's Nutrient Solution

The measurement of nutrients added in solution to the sand medium varied widely by nutrient and by extraction method (Table 1). Cu^{2+} and Fe^{2+} were extracted by all methods in greater net quantities than they were added. This was despite prior sterilization with acetic acid and autoclaving, leaving us to conclude that the sand parent material contained some quantities of readily-extractable Cu^{2+} and Fe^{2+}. None of the methods measured the full supplement of K^+, Zn^{2+}, NO_3^--N, HPO_4^{2-}-P, and SO_4^{2-}S that were added, while Ca^{2+}, Mg^{2+}, Mn^{2+}, and Na^+ were measured in higher amounts by some methods and lower amounts by others than the net μmol_c that was actually added. Proportional to other ions of similar charge, all extraction methods detected high percentages of Ca^{2+}, HPO_4^{2-}-P, and SO_4^{2-}S and low percentages of K^+, Zn^{2+}, and NO_3^--N relative to that which was added.

Among methods in the sand/nutrient solution, chemical extraction represented Ca^{2+} and NO_3^- in the greatest proportions and Cu^{2+}, Fe^{2+}, and K^+ in the least (Table 1). Resin bag extraction represented NH_4^+-N and SO_4^{2-}-S in greatest proportions and Ca^{2+}, Mg^{2+}, NO_3^--N, and Zn^{2+} in the least. Capsules represented Cu^{2+} and K^+ in greatest proportions, and membranes represented Zn^{2+} in the greatest proportions. There were no significant differences among techniques with respect to proportional HPO_4^{2-}-P or Na^+.

In this sand/nutrient solution comparison, all methods determined Na^+ to be the most abundant nutrient (Table 3, Section 1). As suggested by proportional comparisons, the ranking of Cu^{2+}

TABLE 3

Descending order of inorganic nutrients measured by chemical and resin extractions*

Soil/experiment	Method			Order of representation											
(1) Sand/Bolds	Chemical			Na	Ca	Mg	K	HPO_4	NH_4	SO_4	Fe	NO_3	Mn	Zn	Cu
	Resin	Bags		Na	K	NH_4	Ca	HPO_4	SO_4	Mg	Fe	NO_3	Cu	Mn	Zn
		Capsules		Na	K	Ca	HPO_4	Fe	Mg	SO_4	NH_4	NO_3	Cu	Mn	Zn
		Membranes		Na	Ca	K	Mg	HPO_4	Fe	SO_4	NO_3	NH_4	Cu	Zn	Mn
(2) CNP soil—Nakai series	Chemical			Ca	Mg	K	Na	HPO_4	SO_4	Mn	Fe	Cu	Zn		
	Lab resins	Bags	Cold	Ca	Mg	K	NH_4	SO_4	Na	HPO_4	Fe	NO_3	Mn	Cu	Zn
			Warm	Ca	Mg	K	NH_4	Fe	SO_4	Na	HPO_4	Mn	NO_3	Zn	Cu
		Capsules	Cold	Ca	Mg	K	Na	NH_4	SO_4	HPO_4	Fe	Mn	NO_3	Cu	Zn
			Warm	Ca	Mg	K	NH_4	Na	SO_4	Fe	Mn	HPO_4	NO_3	Cu	Zn
		Membranes	Cold	Ca	Mg	K	SO_4	NH_4	Fe	NO_3	HPO_4	Mn	Zn	Cu	
			Warm	Ca	Mg	SO_4	K	Fe	NH_4	Mn	HPO_4	NO_3	Zn	Cu	
	Field resins	Bags		Ca	NH_4	Mg	Fe	Na	SO_4	K	NO_3	HPO_4	Mn	Cu	Zn
		Capsules		Ca	Mg	NH_4	Na	K	Fe	SO_4	NO_3	HPO_4	Zn	Mn	Cu
		Membranes		Ca	Mg	K	NH_4	SO_4	Fe	Mn	NO_3	Zn	HPO_4	Cu	
(3) CNP soil—Sheppard series	Chemical			Ca	Na	Mg	K	SO_4	Mn	Fe	Cu	HPO_4	Zn		
	Lab resins	Bags	Cold	Ca	Mg	NH_4	SO_4	K	Na	Fe	HPO_4	Mn	NO_3	Cu	Zn
			Warm	Ca	Mg	NH_4	K	SO_4	Na	Fe	Mn	HPO_4	NO_3	Cu	Zn
		Capsules	Cold	Ca	Mg	Na	NH_4	K	SO_4	Fe	HPO_4	Mn	NO_3	Cu	Zn
			Warm	Ca	Mg	K	NH_4	Na	SO_4	Fe	Mn	HPO_4	NO_3	Zn	Cu
		Membranes	Cold	Ca	Mg	SO_4	NH_4	K	Fe	NO_3	Mn	HPO_4	Zn	Cu	
			Warm	Ca	Mg	SO_4	NH_4	Fe	K	Mn	HPO_4	NO_3	Zn	Cu	
	Field resins	Bags		Ca	NH_4	Fe	Mg	Na	SO_4	K	NO_3	HPO_4	Mn	Cu	Zn
		Capsules		Ca	NH_4	Na	Mg	K	Fe	SO_4	NO_3	HPO_4	Mn	Zn	Cu
		Membranes		Ca	Mg	SO_4	K	Fe	NH_4	Mn	NO_3	HPO_4	Zn Cu		

*Ranks are based on micromoles of ionic charge (μmol_c). Except for the comparison in sand/nutrient solution, Na^+ data for resin membranes and $NaHCO_3$-charged resins are disregarded. The term "Lab" is used to distinguish from field trials.

was particularly low in chemical extractions and of NH_4^+ was particularly high with bags. All methods desorbed anions in the consistent order HPO_4^{2-}-P > SO_4^{2-}-S > NO_3^--N.

Temperature-Controlled Comparison of Resin Forms in Canyonlands Soil

In temperature-controlled comparisons of CNP soils, there were significant effects of extraction method, temperature, and/or soil source on proportional nutrient representation among all ions but Fe^{2+}, which was not affected by any factor (Table 4). Regardless of soil source, Ca^{2+} was represented in significantly greater proportion and Mg^{2+} in the least proportion by chemical extraction when compared with resin methods (Table 5). SO_4^{2-}-S and Zn^{2+} were represented in the greatest proportions and K^+ and HPO_4^{2-}-P in the least proportions by membranes (Table 5). The proportional representation of other nutrients among methods differed by soil source. For example, in Nakai soils, chemical methods measured greater proportional HPO_4^{2-}-P than SO_4^{2-}-S, a trend that was reversed in the resin data. This reversal of HPO_4^{2-}-P and SO_4^{2-}-S trends did not occur in Sheppard soils. Significant temperature effects (Table 4) generally were due to greater ion sorption in warm conditions than cold (Table 6). Exceptions include Cu^{2+} in Sheppard soils and NO_3^- in soils of either series, which were sorbed in greater quantities in colder temperatures.

All extraction methods reflected greater quantities of K^+, Mg^{2+}, Mn^{2+}, and HPO_4^{2-}-P in Nakai soils (Tables 2, 4, and 6). Some methods resulted in opposite trends between soils. For example, despite higher Ca^{2+} in Nakai soils extracted chemically (Table 2), all resins extracted more Ca^{2+} from Sheppard soils (Tables 4 and 6). Similarly, SO_4^{2-}-S values were greater in Nakai soils as determined by chemical methods ($F = 3818$, $P < 0.001$) and resin membranes ($F = 14.3$, $P = 0.001$) (Tables 2 and 6), but resin bags sorbed greater SO_4^{2-}-S from Sheppard soils ($F = 10.5$, $P = 0.005$).

Among resins only, pooling the effects of temperature and soil source, bags sorbed the most net ionic charge of most nutrients, generally with one of two slightly different patterns (Table 6): Bag > Capsule > Membrane (K^+, HPO_4^{2-}-P; $F = 18.2$ and 20.3, respectively; $P < 0.001$) or Bag > Capsule = Membrane (Ca^{2+}, Fe^{2+}, Mn^{2+}, NH_4^+-N, NO_3^--N, SO_4^{2-}-S; $F = 22.5$, 3.5, 8.0, 120, 4.0, and 196, respectively; $P < 0.05$). Mg^{2+} sorption also followed this Bag > Capsule = Membrane pattern, although statistical signifi-

TABLE 4

F values of MANOVA comparing arcsin-transformed proportions of nutrients extracted by four methods from saturated pastes that varied by soil source.

Nutrient	Resin and chemical extraction[a]						Resins only[b]			
	Extraction method		Soil series		Method × soil series		Temperature		Resin method × temperature	
Ca^{2+}	35.4	***	1725.5	***	19.2	***	1.0		0.1	
Cu^{2+}	77.7	***	132.9	***	80.8	***	19.8	***	0.8	
Fe^{2+}	1.7		1.0		1.4		3.6		1.4	
K^+	53.9	***	185.6	***	32.6	***	1.8		0.6	
Mg^{2+}	71.3	***	3254.2	***	43.4	***	0.1		0.0	
Mn^{2+}	3.2	*	14.1	***	0.2		66.4	***	12.5	***
NH_4^+							12.8	**	4.6	*
Zn^{2+}	25.6	***	3.3		5.6	**	10.6	**	2.0	
NO_3^-							31.1	***	1.4	
HPO_4^{2-}	137.9	***	658.9	***	59.3	***	0.1		0.3	
SO_4^{2-}							8.8	**	0.3	

[a]Proportions were calculated excluding Na^+ data, which were unavailable for resin membranes, and NH_4^+ and NO_3^- data, which were unavailable for chemical extraction. SO_4^{2-}-S and HPO_4^{2-}-P percentages are directly inversely related so only HPO_4^{2-}-P was included in the analysis. Resin data were pooled between temperatures.

[b]Equilibration temperature was manipulated for resin extractions only; NH_4^+ and NO_3^- were therefore included in the proportions calculated for this MANOVA.

*$P < 0.05$;

**$P < 0.01$;

***$P < 0.001$.

TABLE 5

Percentages of nutrients, specific to total positive or negative charge, extracted by conventional ("chemical") methods and by resin bags, capsules, and membranes equilibrating in saturated pastes under controlled environmental conditions*

Nutrient	Nakai series				Sheppard series			
	Chemical	Bags	Capsules	Membranes	Chemical	Bags	Capsules	Membranes
Ca^{2+}	85.4 a	72.5 d	75.7 c	80.2 b	96.2 a	94.6 b	94.6 b	94.6 b
Cu^{2+}	0.008 b	0.009 ab	0.008 b	0.010 a	0.029 a	0.007 d	0.008 c	0.011 b
Fe^{2+}	0.04	1.72	0.30	0.49	0.05 b	0.38 a	0.42 a	0.34 a
K^+	4.7 ab	7.1 a	5.4 b	0.7 c	0.9 b	1.1 b	1.3 a	0.4 c
Mg^{2+}	9.8 b	18.4 a	18.3 a	18.3 a	2.8 d	3.8 b	3.4 c	4.5 a
Mn^{2+}	0.11	0.29	0.27	0.29	0.05	0.15	0.14	0.16
Zn^{2+}	0.007 b	0.008 b	0.005 c	0.015 a	0.010 b	0.004 c	0.011 b	0.018 a
HPO_4^{2-}	61.8 a	25.6 b	28.9 b	17.5 c	16.6 a	12.7 ab	12.1 b	5.5 c
SO_4^{2-}	38.2 c	74.4 b	71.1 b	82.5 a	83.4 c	87.3 bc	87.9 b	94.5 a

*Percentages were calculated without Na^+, NH_4^+, or NO_3^- data (see Methods). Resin data (bags, capsules, and membranes) were pooled between two temperatures (see Methods). Different letters in a row indicate significant ($P < 0.05$) differences among methods within each series.

cance was borderline ($F = 3.0$, $P = 0.06$). Na^+ sorption by bags was also greater than by capsules ($F = 4.4$, $P < 0.05$). Exceptions to the above patterns are Cu^{2+} (Bag > Membrane > Capsule; $F = 36.6$, $P < 0.001$) and Zn^{2+} (Membrane > Bag = Capsule; $F = 14.5$, $P < 0.001$). The greater sorption capacity of bags was also apparent where there were statistical interactions (Table 4). For example, although greater net amounts of Ca^{2+} were sorbed from Sheppard soils ($F = 13.0$, $P = 0.001$), resin bags sorbed more Ca^{2+} ions from Nakai soils than capsules or membranes did from Sheppard soils (Table 6).

All extraction methods in this experiment determined Ca^{2+} to be the most abundant nutrient, and all but chemical extraction of Sheppard soils ranked Mg^{2+} immediately after Ca^{2+} (Table 3, Sections 2 and 3, chemical and lab trials only). SO_4^{2-}-S ranked relatively high in membrane extractions. Among methods, anions were generally extracted in the order SO_4^{2-}-S > HPO_4^{2-}-P > NO_3^--N. Exceptions to this order of anion extraction were cold membrane extraction in either soil, where NO_3^--N > HPO_4^{2-}-P, and chemical extraction of Nakai soils, where HPO_4^{2-}-P > SO_4^{2-}-S. HPO_4^{2-}-P ranked exceptionally low in chemical extractions of Sheppard soils. In Nakai soils, K^+ was the third-ranked nutrient by all methods except membranes in warm conditions. In Sheppard soils, chemical extraction ranked Na^+ higher than any other method.

The ratio of (Ca + Mg):K, an index of ionic competition with K^+ adsorption and activity in solution (Dobermann et al., 1995), was significantly greater ($F = 224.6$, $P < 0.001$) by membrane determination ($F = 189.8$) than any other method ($F = 52.4$), and all methods determined the ratio to be greater in Sheppard than Nakai soils ($F = 229.3$). There were no significant effects of temperature on the index.

Field Comparison of Resin Forms

Proportional nutrient extraction was significantly different among chemical and resin methods in the field for all ions except Zn^{2+} (Table 7). Regardless of soil source, Ca^{2+} and HPO_4^{2-}-P were represented in significantly greater proportion and Mg^{2+} and SO_4^{2-}-S the least proportion by chemical extraction (Table 8). Cu^{2+} was generally extracted in greater proportion by bags and capsules (Table 8). As with the comparison in the controlled environment, proportional representation of most nutrients among methods differed by soil source (Table 7). Significant source effects were generally due to proportionally greater nutrients in Nakai than Sheppard soils, with the exceptions of Ca^{2+} by any method ($F = 56.6$, $P < 0.001$) and Cu^{2+} by chemical extraction ($F = 150.3$, $P < 0.001$), which were proportionally higher in Sheppard series soils.

Among resins only, pooled between the two soil series, there were several patterns of ion behavior among media according to net charge adsorbed (Table 9). Fe^{2+}, NH_4^+, and HPO_4^{2-}-P were sorbed in the order Bags > Capsules = Membranes ($F = 12.4, 6.9$, and 11.4, respectively; $P < 0.01$) (Table 9). SO_4^{2-}-S was sorbed in the order Bags > Membranes > Capsules ($F = 42.2$, $P < 0.001$). Ca^{2+}, Mg^{2+}, and Zn^{2+} followed the pattern Membranes > Bags = Capsules ($F =$

TABLE 6

Mean μmol_c $resin^{-1}$ (SE) nutrients desorbed from resins equilibrating in CNP soil*

Nutrient	Nakai Series								Sheppard Series							
	Cold				Warm				Cold				Warm			
	Bag		Caps	Memb	Bag		Caps	Memb	Bag		Caps	Memb	Bag		Caps	Memb
Ca^{2+}	1189	(174)	892 (82)	931 (20)	1258	(221)	1006 (91)	926 (21)	2517	(268)	1007 (76)	1096 (55)	2590	(145)	1117 (55)	1082 (15)
Cu^{2+}	0.14	(0.01)	0.09 (<0.01)	0.12 (<0.01)	0.13	(0.01)	0.09 (0.01)	0.11 (0.01)	0.19	(0.02)	0.10 (<0.01)	0.13 (0.01)	0.16	(0.01)	0.08 (<0.01)	0.12 (0.01)
Fe^{2+}	6.9	(2.0)	2.5 (0.2)	3.9 (0.5)	47.8	(28.1)	5.0 (0.5)	7.4 (0.5)	6.9	(0.8)	2.9 (0.2)	2.9 (0.1)	13.5	(2.6)	6.7 (0.5)	5.0 (0.3)
K^{+}	89.2	(2.0)	48.5 (1.0)	9.5 (0.3)	140.1	(13.9)	87.6 (5.7)	7.8 (0.1)	23.7	(1.2)	11.6 (0.2)	5.4 (0.2)	33.8	(1.2)	18.6 (0.5)	4.1 (0.2)
Mg^{2+}	289	(30)	200 (13)	203 (5)	331	(68)	260 (23)	221 (4)	92.3	(9.7)	34.2 (2.0)	48.6 (2.7)	110.9	(5.2)	43.1 (1.3)	54.1 (0.8)
Mn^{2+}	3.6	(0.6)	2.2 (0.2)	0.9 (0.1)	6.5	(1.1)	4.7 (0.5)	5.8 (0.1)	3.4	(0.4)	1.1 (0.1)	0.7 (0.1)	4.8	(0.2)	2.0 (0.1)	3.1 (0.1)
Na^{+}	17.4	(1.1)	15.5 (0.3)		17.2	(2.0)	14.9 (0.8)		13.8	(0.3)	13.2 (0.4)		14.5	(1.6)	12.1 (1.0)	
NH_4^{+}	44.5	(7.6)	10.3 (1.6)	6.6 (0.6)	98.8	(7.8)	26.2 (5.5)	6.8 (0.7)	68.4	(2.2)	12.1 (0.2)	7.5 (0.7)	88.1	(3.7)	16.3 (1.0)	8.5 (0.2)
Zn^{2+}	0.1	(0.02)	0.1 (0.01)	0.1 (0.01)	0.1	(0.03)	0.1 (<0.01)	0.2 (0.01)	0.1	(0.01)	0.1 (0.05)	0.2 (0.01)	0.1	(0.02)	0.2 (0.02)	0.03 (0.02)
NO_3^{-}	5.0	(1.2)	2.0 (0.2)	2.4 (0.3)	1.5	(0.4)	0.7 (0.2)	0.4 (0.1)	1.3	(0.3)	0.7 (0.4)	1.1 (0.4)	0.7	(0.1)	0.5 (0.2)	0.4 (0.1)
HPO_4^{2-}	8.4	(1.3)	4.3 (0.4)	2.2 (0.1)	7.1	(2.2)	4.7 (0.4)	2.0 (0.1)	4.2	(0.5)	1.3 (0.1)	0.5 (<0.1)	3.5	(0.3)	1.4 (0.1)	0.6 (<0.1)
SO_4^{2-}	21.0	(0.9)	9.9 (0.5)	9.3 (0.2)	21.7	(2.2)	12.2 (1.0)	10.2 (0.2)	25.0	(1.6)	8.8 (0.4)	8.8 (0.4)	27.2	(0.8)	10.3 (0.3)	8.7 (0.1)

$N = 5$.

23.1, 8.4, and 21.0; $P < 0.01$) and Cu^{2+} and Mn^{2+} were sorbed in the order Membranes > Bags > Capsules (F = 33.5 and 25.0, $P < 0.001$). The only nutrients whose sorption patterns among resin forms in the field corresponded to that in the controlled experiments were Fe^{2+}, NH_4^{+}-N, and Zn^{2+}.

Similar to the other comparisons of extraction methods, resins in the field determined Ca^{2+} to be the most abundant nutrient (Table 3, Sections 2 and 3, chemical and field trials). The rank of K^{+} was highest for chemical and membrane extraction and fell with increasing resin sorption capacity (rank of Bag_{K+} > $Capsule_{K+}$ < $Membrane_{K+}$). Similar to laboratory results, SO_4^{2-}-S ranked relatively high in membrane extractions, and NH_4^{+}-N ranked relatively low. Also, anions were usually extracted in the order SO_4^{2-}-S > NO_3^{-}-N > HPO_4^{2-}-P, except for chemical extraction of Nakai soils, where HPO_4^{2-}-P > SO_4^{2-}-S. Again, HPO_4^{2-}-P was exceptionally low in chemical extractions of Sheppard soils.

Also similar to nonfield trials were trends of (Ca + Mg):K. The (Ca + Mg):K ratio was significantly ($P < 0.001$) greater for membranes than for bags or capsules (F = 37.4) and was greater in Sheppard than in Nakai soils (F = 121.6).

TABLE 7

F values of MANOVA comparing the proportional amount of nutrients extracted by resins in the field at CNP and conventional chemical extractions[a]

Nutrient	F values		
	Method	Soil series	Method × soil series
Ca^{2+}	98.5 ***	514.2 ***	8.8 ***
Cu^{2+}	9.6 ***	0.2	0.9
Fe^{2+}	13.7 ***	0.0	0.1
K^{+}	27.8 ***	88.9 ***	2.8
Mg^{2+}	31.3 ***	449.4 ***	17.2 ***
Mn^{2+}	14.9 ***	24.8 ***	7.6 **
Zn^{2+}	2.7	4.3 *	0.8
HPO_4^{2-} SO_4^{2-}	375.0 ***	230.8 ***	177.9 ***

[a]Proportions were calculated excluding Na^{+}, NH_4^{+}-N and NO_3^{-}-N data. SO_4^{2-}-S and HPO_4^{2-}-P percentages are directly inversely related so only HPO_4^{2-}-P was included in the analysis.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

TABLE 8

Percentages of nutrients, specific to total positive or negative charge, extracted by conventional ("chemical") methods and by resin bags, capsules, and membranes equilibrating in the field at CNP*

Nutrient	Nutrient percentages							
	Nakai Series				Sheppard Series			
	Chemical	Bag	Capsule	Membrane	Chemical	Bag	Capsule	Membrane
Ca^{2+}	85.4 a	62.0 c	69.0 b	72.0 b	96.2 a	83.2 c	85.0 c	94.2 b
Cu^{2+}	0.01 c	0.08 abc	0.09 a	0.04 b	0.03 b	0.08 a	0.07 a	0.02 c
Fe^{2+}	<0.1 c	7.7 abc	3.0 a	1.2 b	0.1 d	8.1 a	3.5 b	0.4 c
K^+	4.7 b	6.4 ab	8.7 a	2.7 c	0.9 c	1.9 b	3.9 a	0.7 c
Mg^{2+}	9.8 c	23.5 a	19.0 b	23.8 a	2.8 c	6.4 a	7.3 a	4.6 b
Mn^{2+}	0.1 b	0.3 a	0.1 b	0.2 a	0.05 b	0.17 a	0.13 ab	0.08 b
Zn^{2+}	0.01	0.08	0.12	0.09	0.01 c	0.06 a	0.05 a	0.03 b
HPO_4^{2-}	61.8 a	6.1 b	6.3 b	5.1 b	16.6 a	4.5 bc	7.7 b	4.2 c
SO_4^{2-}	38.2 b	93.9 a	93.7 a	94.9 a	83.4 c	95.5 ab	92.3 b	95.8 a

*Percentages were calculated without Na^+, NH_4^+, or NO_3^- data. Different letters in a row indicate significant ($P < 0.05$) differences among methods within each soil series.

DISCUSSION

Our results show that the four different extraction techniques are not comparable. Even a cursory comparison of nutrient rankings by their abundance reveals large differences among the methods (Table 3). Soil source affects this comparison, indicated by closer agreement of rankings among methods in Nakai series soils than in Sheppard series soils.

Methods varied not only in their net extraction of nutrients but in proportional extraction as well (Tables 1, 5, and 8), and soil source and/or experimental conditions also had an effect on extraction. For example, proportional HPO_4^{2-}-P was not different among methods in sand/nutrient solution (Table 1), but did show significant differences among methods in both lab and field trials using CNP soils (Tables 4 and 7). Similarly, Zn^{2+} was not different among the methods in the field (Table 7) but was different among the methods in nonfield trials (Tables 1 and 4). Differences in equilibration time and in soil moisture (Yang et al., 1991a) probably contributed to the differences in laboratory and field results. Soil moisture in the field, never higher than 15.5% (in Nakai soils), was far less than that of the saturated pastes used in the temperature-controlled trials.

Exchange capacity (Bags > Capsules > Membranes) and ion affinities explain some of the patterns of net nutrient sorption among the resins as measured in μmol_c. Resin cation affinities occur in the order $Ca^{2+} > Mn^{2+} > Cu^{2+} >$

TABLE 9

Means (μmol_c $resin^{-1}$) and SE of nutrients sorbed by resins in field trials

Nutrient	Nakai series						Sheppard series					
	Bags		Caps		Memb		Bags		Caps		Memb	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Ca^{2+}	132	31	79	9	361	72	135	10	106	20	958	35
Cu^{2+}	0.13	0.02	0.10	<0.01	0.17	<0.01	0.13	0.01	0.08	<0.01	0.19	0.01
Fe^{2+}	13.8	4.4	3.2	0.2	5.1	0.6	13.4	3.5	4.1	0.5	4.3	0.7
K^+	11.6	0.8	10.1	1.6	12.9	1.6	3.2	0.5	4.9	1.0	6.6	1.1
Mg^{2+}	51.4	13.2	21.4	2.4	121.8	26.8	10.6	1.3	9.2	1.7	46.9	3.9
Mn^{2+}	0.6	0.2	0.1	<0.1	1.1	0.1	0.3	<0.1	0.2	<0.1	0.8	0.1
Na^+	12.4	0.2	11.2	0.3			10.1	0.9	10.7	0.5		
NH_4^+	86.4	31.6	13.2	4.2	6.6	3.8	48.9	21.7	35.7	25.9	1.3	0.3
Zn^{2+}	0.1	0.03	0.1	0.04	0.4	0.06	0.1	0.01	0.1	0.02	0.3	0.02
NO_3^-	1.3	0.4	0.7	0.1	0.5	0.1	0.4	0.1	0.8	0.3	0.3	0.1
HPO_4^{2-}	0.8	0.1	0.2	<0.1	0.3	<0.1	0.4	<0.1	0.2	<0.1	0.3	<0.1
SO_4^{2-}	11.6	0.2	3.2	0.2	5.4	0.3	8.0	1.1	3.0	0.4	7.1	0.5

$Zn^{2+} \equiv Mg^{2+} > Fe^{2+} \geq K^{+} > NH_4^{+} > Na^{+} > H^{+}$ (Skogley and Dobermann, 1996). In two of our experiments, higher affinity ions were sorbed in greater net amounts by nutrient membranes than the other two resin types: Ca^{2+}, Mg^{2+}, Mn^{2+}, and Zn^{2+} in the sand/nutrient solution trial ($F = 74.8$, 39.3, 40.4, and 408, respectively) (Table 1) and Ca^{2+}, Cu^{2+}, Mg^{2+}, Mn^{2+}, and Zn^{2+} in the field trial ($F = 23.1, 33.5$, 8.4, 25.0, and 21.0) (Table 9). We attribute the greater representation of these cations on membranes than on bags or capsules to their higher resin affinities, the lower exchange capacity of resin membranes, and sufficient duration for ionic affinities to differentiate. The low-affinity cations Fe^{2+} and NH_4^{+}-N were sorbed in the greatest quantities by resin bags ($F > 3.5$, Fe^{2+} and $F > 6.9$, NH_4^{+}) (Tables 6 and 9), where they should persist longer until replaced by higher affinity ions.

We observed an apparent relationship between Ca^{2+} and NH_4^{+}-N, whose sorption patterns among the three resin forms were opposite. In the sand/nutrient solution trial, Ca^{2+} constituted increasing proportions of total positive charge with decreasing exchange capacity (i.e., 12.4%, 15.3%, and 25.8% of the total positive charge of bags, capsules, and membranes, respectively) (Table 1). In the same experiment, NH_4^{+}-N represented decreasing proportions of the same (i.e., 15.1%, 4.6%, and 0.9% of bags, capsules, and membranes, respectively). Not only do the patterns of Ca^{2+} and NH_4^{+}-N sorption mirror each other in this trial, but their net differences in proportional representation between bags and membranes are approximately equal at 13% to 14%. The high resin affinity of Ca^{2+} (Skogley and Dobermann, 1996) is apparent in its high adsorption to resin membranes relative to their exchange capacity. Cation loading of exchange sites in bags and capsules probably had not approached capacity in the week-long equilibration, hence their lower representation of Ca^{2+}. NH_4^{+}-N is a cation of low resin affinity and its behavior among resin types can be explained by the same principle. Ca^{2+}-NH_4^{+} trends were also opposite in both laboratory and field experiments with CNP soil except in Sheppard soils in laboratory experiments (Tables 5 and 8).

Nutrient sorption trends in nonfield analyses using CNP soils (Tables 4–6), however, cannot be universally explained using this argument of resin exchange capacity and ion affinities, probably due to insufficient equilibration duration (1 week) to allow ion affinities to become distinct. In this case, bags sorbed the greatest net amounts of most nutrients (Table 6). Our results are similar to the 16-h incubation of Saggar et al. (1990) and the 24-h incubation of Fernandes and Warren (1996), but contrast to Nuernberg et al. (1998), who found that resin bags and AEMs extracted roughly equivalent amounts of P from solution during incubations of 2 to 65 h.

Between soil series, only the trends of K^{+} and Mg^{2+} were consistent among methods and experiments (Tables 2, 6, and 9), and resin-Ca^{2+} and -Na^{+} trends between the two soils were contrary to those determined by chemical procedures. Ca^{2+} was higher in Nakai soils by chemical methods ($F = 30.1$, $P < 0.001$) (Table 2) and in Sheppard soils by resin methods ($F = 4.5$, lab; $F = 13.0$, field; Tables 6 and 9), a discrepancy of particular concern in this semiarid ecosystem that contains areas of exceptionally high soil Ca^{2+}. We suspect measurement error in the chemical extraction of Ca^{2+}. It is possible, for example, that the ammonium acetate extraction used to measure Ca^{2+} even at pH 8.5 (Normandin et al., 1998) dissolves some of the small particulate concretions of $CaCO_3$ that occur in finer-grained Nakai soils, resulting in an erroneously high estimate of exchangeable Ca^{2+}. This should be taken into account when considering NH_4OAc extraction of other carbonate-related nutrients, particularly in high-carbonate soils. In contrast, Na^{+} by chemical methods was slightly higher in Sheppard soils ($F = 4.7$, $P = 0.06$) (Table 2) but higher in Nakai soils by resin extraction ($F = 13.1$, lab; $F = 7.0$, field) (Tables 6 and 9). This contradiction may be due to competitive displacement of low-affinity Na^{+} by high-affinity and more abundant Ca^{2+} on resins in the Sheppard soils.

Our results generally show stimulation of ionic diffusion with higher equilibration temperatures, similar to the findings of Schaff and Skogley (1982), Skogley et al. (1990), and Yang et al. (1991b) with respect to Mn^{2+}, NH_4^{+}-N, SO_4^{2-}-S, and Zn^{2+} (Tables 4 and 6). An exception to this response is NO_3^{-}-N (Tables 4 and 6), which showed greater adsorption at colder temperatures. This NO_3^{-}-N response to cold temperatures corroborates Yang et al. (1991b) and Lundell (1989), and in these saturated soils could be due to increased denitrification with higher temperatures (Yang et al., 1991b). Temperatures over the 94-day field incubation approximately spanned the ranges tested in both cold and warm laboratory incubations, making it difficult to compare the effects of temperature in this experiment to those in the temperature-controlled experiment.

The lower temperatures and higher soil moisture of CNP during winter can result in higher CO_2 solubility and subsequent formation of carbonic acid ($CO_2 + H_2O \leftrightarrow H_2CO_3$) (Birkeland, 1984; Krauskopf and Bird, 1995). This in turn can affect the availability of $CaCO_3$-bound ions that typically peak during winter months (Schaff and Skogley, 1982; Lajtha, 1988; Lundell, 1989). Increasing formation of H_2CO_3 with decreasing temperature should account for some dissolution and increased sorption of carbonate-related ions such as Ca^{2+}, Mg^{2+}, Mn^{2+}, HPO_4^{2-}-P, and Zn^{2+} (Schaff and Skogley, 1982; Lundell, 1989), but this was not observed in this study. The sorption trends of Ca^{2+}, Mg^{2+}, and HPO_4^{2-}-P between temperatures were inconsistent and/or statistically insignificant among resins, and Mn^{2+} and Zn^{2+} were sorbed in greater quantities at higher temperatures (Tables 4 and 6). Lower carbonate solubilities and higher diffusion rates at high temperatures may counteract each other, yielding a lack of sensitivity to temperature, as Schaff and Skogley (1982) theorized with respect to Mg^{2+}. In contrast, it is possible that in an ecosystem with respiring roots and unrestricted gas exchange such as CNP, which supports wintertime growth, we would observe higher sorption of these ions at colder temperatures (e.g., Lundell, 1989).

As suggested above, multiple-element exchange with soil colloids and ion-exchange resins is saddled with interdependent dynamics (Curtin et al., 1987; Subler et al., 1995; Skogley and Dobermann, 1996) despite assertions to the contrary (Lajtha, 1988; Skogley et al., 1990; Yang et al., 1991a). In our soils, Ca^{2+} is by far the ion in greatest supply (Table 3) and, by virtue of its high affinity (Skogley and Dobermann, 1996), is an effective competitor for resin exchange sites. Resin membranes had significantly higher (Ca + Mg):K ratios than any other method in both field and laboratory trials, accounted for by Ca^{2+}-resin affinity and low membrane sorption capacity. This index of biological K^+ activity (Dobermann et al., 1995) is particularly important for biogeochemical measurements at CNP, where invasive species are associated with relatively high levels of exchangeable soil K^+ (Belnap and Phillips, 2001). Our comparisons of nutrient availability determined by different resin forms reinforce the proposition that sorption capacity and equilibration duration are interacting factors that need to be accounted for in experimental design.

While true that ion-exchange resins are dynamic nutrient exchangers (Christensen and Posner, 1980; Cooperband and Logan, 1994; Skogley and Dobermann, 1996), sufficient duration of resin equilibration relative to its ion exchange capacity apparently allows ions of higher affinity to sorb preferentially to resin exchange sites. With respect to high-affinity ions, therefore, ion-exchange resins act as nutrient sinks (Lundell, 1989; Yang, 1991b). Different exchange capacities and ion affinities among resins should be taken into account in constructing research design and methods.

We also call attention to the possibility of inaccuracies of any extraction method measuring multiple nutrients, as demonstrated by comparisons between known amounts of nutrients added and those extracted (Table 1). If the goal is to represent plant-available nutrients in an ecosystem, it is advisable to identify which nutrients are of foremost interest and understand differences in their resin sorption dynamics, and to identify the appropriate resin-soil equilibration period, which will help determine the appropriate extraction method to employ. Resin bags, with their greater charge capacity, may create a diffusion gradient affecting strongly-sorbed nutrients such as Ca^{2+} and HPO_4^{2-}-P more than capsules or membranes (Saggar et al., 1990; Dobermann et al., 1995). In contrast, the larger exchange capacity of resin bags and capsules may simulate the strong nutrient sink created by a plant, but perhaps within a shorter equilibration time frame. Indeed, when used in the soils of plant communities, a small degree of nutrient competition may be expected between vegetation and ion-exchange resins, although this has not been observed to impede plant growth (Binkley, 1984; Lundell, 1989).

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Comparison of Ion-Exchange Resin Counterions in the Nutrient Measurement of Calcareous Soils: Implications for Correlative Studies of Plant–Soil Relationships[#]

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ABSTRACT

For more than 40 years, ion-exchange resins have been used to characterize nutrient bioavailability in terrestrial and aquatic ecosystems. To date, however, no standardized methodology has been developed, particularly with respect to the counterions that initially occupy resin exchange sites. To determine whether different resin counterions yield different measures of

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soil nutrients and rank soils differently with respect to their measured nutrient bioavailability, we compared nutrient measurements by three common counterion combinations (HCl, HOH, and $NaHCO_3$). Five sandy calcareous soils were chosen to represent a range of soil characteristics at Canyonlands National Park, Utah, and resin capsules charged with the different counterions equilibrated in saturated pastes of these soils for one week. Data were converted to proportions of total ions of corresponding charge for ANOVA. Results from the different methods were not comparable with respect to any nutrient. Of eleven nutrients measured, all but iron (Fe^{2+}), manganese (Mn^{2+}), and zinc (Zn^{2+}) differed significantly ($p \leq 0.05$) as a function of soil × counterion interactions; Fe^{2+} and Zn^{2+} varied as functions of counterion alone. Of the counterion combinations, HCl-resins yielded the most net ion exchange with all measured nutrients except Na^+, NH_4^+, and HPO_4^{2-}, the three of which desorbed in the greatest quantities from HOH-resins. Conventional chemical extractions using ammonium acetate generally yielded high proportional values of Ca^{2+}, K^+, and Na^+. Further, among-soil rankings of nutrient bioavailability varied widely among methods. This study highlights the fact that various ion-exchange resin techniques for measuring soil nutrients may have differential effects on the soil-resin environment and yield data that should not be compared nor considered interchangeable. The most appropriate methods for characterizing soil-nutrient bioavailability depends on soil characteristics and likely on the physiological uptake mechanisms of plants or functional groups of interest. The effects of different extraction techniques on nutrient measures should be understood before selecting an extraction method. For example, in the calcareous soils used for this experiment, nutrient extraction methods that alter soil carbonates through dissolution or precipitation could compromise the accurate measurement of plant-available nutrients. The implications of this study emphasize the universal importance of understanding the differential effects of alternate methods on soil chemistry.

Key Words: Ion-exchange resins; Counterions; Calcareous soils; Nutrient extraction method.

INTRODUCTION

Measuring plant-available soil nutrients with sensitivity to variation in soil properties is an ongoing challenge. Chemical extractions are conventional for measuring nutrient bioavailability but ion-exchange resins, demonstrated to be effective measures of soil nutrients in both terrestrial and aquatic ecosystems,[1-3] may be preferable in some studies (see Skogley and Dobermann[4] for review). Chemical extraction provides a static measure of

potential nutrient supply,[5] in contrast to resins which, as ionic exchangers, represent an integration of bioavailable nutrient dynamics during a specified incubation period.[4,6,7] In addition, resins are sensitive to environmental conditions,[8,9] more efficient at measuring multiple soil nutrients than performing an equivalent number of chemical extractions,[10] inexpensive, and nondestructive with respect to soil chemistry and mineralogy.[7]

Resins have been compared to both soil colloids[4,7] and plant roots.[1,11,12] The acidification effect of resins with desorption of a H^+ countercation is similar to that of plant roots, although whether it occurs in comparable quantities is unknown. Also similar to root processes are the effects of cation uptake on that of anions and vice versa due to charge–balance relations and shifts in soil equilibria.[1,13] The dynamic colloidal effects of resins, however, are like that of soil. Hence, ion-exchange resins embody characteristics of both biological and mineral components of soil ecosystems.

Despite the application of ion-exchange resins for more than 40 years[14] and their general acceptance as a method for detection of soil nutrient levels, methods of resin use among researchers are not uniform and the interpretive differences among methods are poorly understood. The focus of this study is whether different resin counterions, which desorb from ion-exchange resins in exchange for nutrient ions of equivalent charge from the equilibrating solution, yield different nutrient measurement data. For example, different counterions have been identified as the best exchangers for solution P. These include bicarbonate (HCO_3^-)[15–17] OH^-[18–20] Cl^-,[6] and acetate (CH_3COO^-).[21] The soils used in the cited studies varied widely in their chemical, mineralogical, and physical characteristics, indicating that the best resin counterion for P exchange is a function of inherent soil properties.[15] For correlative ecological studies where among-soil variations in plant community composition are analyzed in relation to among-soil variations in soil nutrient bioavailability, it is critical to ascertain whether among-soil rankings of nutrient bioavailability are dependent on initial resin counterions.

We compared the results of soil nutrient measurements by three different resin counterion combinations in calcareous soils from the Canyonlands National Park (CNP), southeast Utah, USA. Carbonates are high in CNP soils (Table 1) and are sensitive to the changes in moisture, temperature, and pH[1,16,22] that can be induced by various extraction techniques. We included data from single measures ($n = 1$) of soil nutrients from conventional chemical extraction techniques. Although statistical tests with these data were precluded by the singular samples, it offers a useful comparison.

Table 1. Soil characteristics of five sites from which soils were taken for resin counterion comparisons. Samples (n = 1) were taken from 0–10 cm depth. Soil group nomenclature is from the U.S.D.A. soil taxonomy. Data are from Miller.[23]

Site	Soil group	% sand	% silt	% clay	Texture class	Bulk density ($g\,cm^{-3}$)	pH	EC ($dS\,m^{-1}$)	Carbonates (% $CaCO_3$ equiv.)	CEC ($cmol_c\,kg^{-1}$)	OM (%)
1	Mesic Ustollic Camborthid	77.3	17.0	5.7	Loamy sand	1.46	7.35	0.46	5.11	8.74	0.24
2	Mesic Typic Torripsamment	87.9	8.0	4.1	Sand	1.50	7.73	0.44	6.21	4.83	0.29
3	Mesic Typic Torripsamment	89.0	7.3	3.4	Sand	1.51	7.60	0.43	5.02	3.00	0.14
4	Mesic Ustollic Camborthid	82.2	12.8	5.0	Loamy sand	1.52	7.50	0.39	6.46	6.83	0.39
5	Mesic Ustollic Camborthid	79.8	15.0	5.2	Loamy sand	1.51	7.50	0.42	5.59	5.13	0.39

METHODS

Five sites representing a range of soil characteristics (Table 1) were selected for soil sampling in CNP (~1500 m a.s.l.), a cold semiarid ecosystem in eastern Utah averaging 214 mm annual precipitation and 11.6°C annual temperature.[23] Aggregate soil samples (0–10 cm) were collected from each site on 14 December 1999. At the Soil and Plant Analysis Laboratory (SPAL) at Brigham Young University (Provo, UT), soils were analyzed for ammonium acetate (NH_4OAc)-extractable calcium, potassium, magnesium, and sodium at pH 8.5 (Ca^{2+}, K^+, Mg^{2+}, and Na^+),[24] DTPA-extractable copper, iron, manganese, and zinc (Cu^{2+}, Fe^{2+}, Mn^{2+}, and Zn^{2+}),[25] KCl-extractable inorganic nitrogen (NH_4^+ and NO_3^-), and bicarbonate-extractable phosphorus (HPO_4^{2-}).[26] N = 1 for conventional chemical analysis.

Forty-five mixed-bed (bipolar) resin capsules (WECSA, Fort Collins, CO) originally charged with H^+ and OH^- ions were divided into three groups and charged with 0.5 M HCl, 0.5 M $NaHCO_3$, or nothing, in which case they remained charged with H^+ and OH^-. Capsules were ionically charged by shaking them in solution for 2 h with the solution replaced halfway through the shake period. Three replicates of resin capsules in each of the three ionic forms were equilibrated for 1 wk in saturated pastes[27] of the five soils. Ions were desorbed from all resins in 2 *M* HCl for 1 h and all except inorganic N were measured by inductively coupled plasma spectrometry. NH_4^+ and NO_3^- were determined by titration with H_2SO_4. Results were reported in $\mu g\ capsule^{-1}$ and converted to μmol of charge $capsule^{-1}$ (μmol_c).

Because the volume of soil subject to measurement by ion-exchange resins is unknown and each counterion combination extracts different quantities of ions, we converted all data to proportions of total ions of corresponding charge. For example, proportional NO_3^- was calculated as $(\mu mol_c\ NO_3^-)/(\mu mol_c\ NO_3^- + \mu mol_c\ HPO_4^{2-} + \mu mol_c\ SO_4^{2-})$. Sodium ($Na^+$) is over-represented on $NaHCO_3$-charged resins and sulfate (SO_4^{2-}) data were unavailable for chemical extractions; these were disregarded for proportional calculations. We arcsin-transformed proportional data and tested for differences in proportional nutrient representation among the resins charged with different counterions with multivariate ANOVA. No statistical comparisons between resin and chemical methods were made because there were no replicates of chemical extractions. All statistics were analyzed using SPSS Release 6.1.3. Unless otherwise stated, all significance refers to $p < 0.05$. To provide another, potentially clearer, way of interpreting the data, we constructed two rankings, one of CNP sites according to the nutrient quantities extracted by the different methods, and one of nutrients desorbed with each method.

RESULTS

Evaluating resin data only, all nutrients were extracted in significantly different proportions among different counterions (Table 2), and most showed significant interactions between counterion and site. There were significant differences among sites in the proportional representation of all nutrients except for Fe^{2+} and Zn^{2+}.

Among resins only, HCl-charged resins consistently extracted the greatest total amount of nutrient cations, even excluding Na^+ ($F = 390$, $p < 0.001$). HOH- and $NaHCO_3$-resins extracted decreasing amounts of cations (Table 3a–e). HCl-resins also extracted the greatest amounts of anions ($F = 178$, $p < 0.001$) with the exception of Sites 1 and 4, where there were no significant differences between anion extraction by HCl- and HOH-resins.

Patterns of net extraction of specific nutrients varied among resin forms. Mg^{2+}, Mn^{2+}, and SO_4^{2-} were extracted in the order HCl > HOH > $NaHCO_3$ at all sites ($F = 79.1$, 124, and 298, respectively; $p < 0.001$), as were Ca^{2+} and Cu^{2+} ($F = 318$ and 271; $p < 0.001$) except in Site 1 soils. Although differences were not always significant, K^+ and HPO_4^{2-} net

Table 2. F values of multivariate ANOVA comparing the proportional amount of nutrients extracted by resins with three counterion combinations from five different soil sources. All data were arcsin-transformed. Cation proportions were calculated excluding Na^+ data, which were unavailable for $NaHCO_3$ counterions. Chemical proportions were not included in this analysis because N = 1 for chemical extractions. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

	Site	Counterions	Site × counterions
Ca^{2+}	134***	19.1***	2.5*
Cu^{2+}	19.5***	140***	2.6*
Fe^{2+}	1.5	30.7***	0.8
K^+	125***	64.6***	10.6***
Mg^{2+}	98.5***	25.0***	2.6*
Mn^{2+}	4.7**	92.6***	1.5
NH_4^+	37.3***	150***	14.0***
Zn^{2+}	0.8	20.6***	1.9
NO_3^-	18.5***	6.3**	4.6**
HPO_4^{2-}	7.6***	117***	2.8*
SO_4^{2-}	26.0***	54.7***	4.7**

Table 3. Mean, standard error (SE), and percent nutrients in CNP soils determined by chemical extraction and resin capsules charged with three different counterion combinations. Means are expressed in $\mu mol_c\ kg^{-1}$ for chemical extraction and $\mu mol_c\ capsule^{-1}$ for resin extraction. Percentages are relative to total positive or negative charge, disregarding Na^+ for cations and SO_4^{2-} data for anions. Different letters indicate significant differences ($p < 0.05$) among percentages for resin data only. N = 3 for resins. Dashes indicate that a value was not determined.

			Resin capsule counterions											
	Chemical		HCl				HOH				$NaHCO_3$			
Nutrient	Mean	%	Mean	SE	%		Mean	SE	%		Mean	SE	%	
a. Site 1														
Ca^{2+}	2940	86.1	1870	95.5	86.4	NS	923	96.4	82.3	NS	597	99.0	86.0	NS
Cu^{2+}	0.6	0.02	0.9	0.02	0.041	c	0.5	0.05	0.047	b	0.4	0.07	0.054	a
Fe^{2+}	1.3	<0.1	8.3	1.1	0.4	NS	4.2	0.7	0.4	NS	7.0	3.3	0.9	NS
K^+	324	9.5	35.6	13.6	1.7	b	46.0	2.6	4.1	a	25.5	1.0	3.8	ab
Mg^{2+}	138	4.0	204	19.4	9.5	NS	115	11.2	10.3	NS	56.3	7.6	8.2	NS
Mn^{2+}	2.8	0.1	36.3	6.6	1.7	a	20.7	2.0	1.9	a	4.0	2.6	0.5	b
Na^+	57.3	—	7.2	5.2	—		10.0	0.8	—		—	—	—	
NH_4^+	9.1	0.3	5.4	2.4	0.2	b	10.8	1.8	1.0	a	3.2	0.6	0.5	b
Zn^{2+}	0.2	0.01	0.3	0.02	0.01	b	0.2	0.01	0.02	b	0.2	0.02	0.03	a
NO_3^-	0.5	6.3	2.3	0.6	30.7	a	0.8	0.2	10.6	b	1.0	0.2	25.3	a
HPO_4^{2-}	6.7	93.7	5.0	0.6	69.3	b	6.6	0.8	89.4	a	2.9	0.5	74.7	b
SO_4^{2-}	—	—	12.7	0.3	—		8.6	0.8	—		5.3	0.7	—	
Total cations	3480		2160				1130				—			
Total anions	—		20.0				16.0				9.1			

(continued)

Table 3. Continued.

			Resin capsule counterions											
	Chemical		HCl				HOH				$NaHCO_3$			
Nutrient	Mean	%	Mean	SE	%		Mean	SE	%		Mean	SE	%	
b. Site 2														
Ca^{2+}	2520	90.7	1840	73.4	87.8	a	1130	60.5	86.0	b	525	5.7	86.8	ab
Cu^{2+}	0.3	0.01	0.8	0.03	0.040	c	0.6	0.02	0.043	b	0.3	0.01	0.048	a
Fe^{2+}	4.0	0.1	6.8	0.8	0.3	b	3.0	0.2	0.2	b	4.2	0.4	0.7	a
K^{+}	168	6.0	41.5	1.4	2.0	b	40.8	1.1	3.1	a	22.3	1.6	3.7	a
Mg^{2+}	76.1	2.7	174	8.7	8.3	a	107	6.4	8.1	a	44.8	1.8	7.4	b
Mn^{2+}	1.5	0.1	26.1	0.7	1.2	b	22.1	1.7	1.7	a	2.8	0.5	0.5	c
Na^{+}	52.9	—	3.4	0.8	—		11.1	0.6	—		—	—	—	
NH_4^{+}	9.7	0.3	6.3	0.1	0.3	b	11.4	1.1	0.9	a	5.2	0.3	0.9	a
Zn^{2+}	0.2	0.01	0.3	0.02	0.01	b	0.2	<0.01	0.01	b	0.2	0.01	0.03	a
NO_3^{-}	0.6	6.2	3.2	0.3	41.0	a	0.6	0.2	9.8	c	0.6	<0.1	20.0	b
HPO_4^{2-}	8.9	93.8	4.6	0.1	59.0	c	5.5	0.3	90.2	a	2.5	0.1	80.0	b
SO_4^{2-}	—	—	13.1	0.4	—		10.0	0.5	—		5.0	<0.1	—	
Total cations	2830		2100				1330				—			
Total anions	—		20.9				16.1				8.2			
c. Site 3														
Ca^{2+}	2500	93.3	2000	75.5	91.8	NS	1050	62.9	91.4	NS	434	13.5	92.0	NS
Cu^{2+}	0.3	0.01	0.8	0.02	0.036	b	0.5	0.03	0.043	a	0.2	0.01	0.048	a
Fe^{2+}	8.3	0.3	7.0	0.7	0.3	b	2.8	0.6	0.2	b	4.0	0.7	0.8	a
K^{+}	111	4.1	27.1	0.4	1.3	NS	15.6	2.1	1.4	NS	6.5	0.4	1.4	NS

Mg^{2+}	50.7	1.9	110	4.0	5.0	a	54.6	4.1	4.7	b	21.5	0.7	4.6	b
Mn^{2+}	1.0	<0.1	26.0	1.6	1.2	a	15.3	1.9	1.3	a	1.8	0.5	0.4	b
Na^{+}	64.1	—	4.8	0.7	—		8.5	0.6	—		—	—	—	
NH_4^{+}	8.8	0.3	8.2	0.1	0.4	b	10.0	1.2	0.9	a	3.7	0.6	0.8	a
Zn^{2+}	0.2	0.01	0.6	0.2	0.03	NS	0.2	0.02	0.01	NS	0.1	0.01	0.03	NS
NO_3^{-}	4.0	36.4	1.7	0.2	28.3	a	0.6	<0.1	12.6	b	0.5	<0.1	22.8	a
HPO_4^{2-}	7.1	63.6	4.2	<0.1	71.7	b	4.3	0.2	87.5	a	1.8	<0.1	77.2	b
SO_4^{2-}	—	—	13.0	0.5	—		8.7	0.3	—		3.7	0.1	—	
Total cations	2750		2180				1160				—			
Total anions	—		18.9				13.6				6.0			
d. Site 4														
Ca^{2+}	2720	90.7	1810	156	87.1	a	1110	33.6	85.2	b	432	14.7	86.0	b
Cu^{2+}	0.4	0.01	0.8	0.05	0.041	c	0.6	0.01	0.047	b	0.3	0.02	0.059	a
Fe^{2+}	1.6	0.1	6.6	0.3	0.3	b	3.8	0.5	0.3	b	3.0	0.2	0.6	a
K^{+}	178	5.9	36.0	1.2	1.8	c	33.8	0.4	2.6	b	16.8	0.3	3.4	a
Mg^{2+}	89.7	3.0	186	20.0	8.9	a	116	3.5	8.9	a	38.2	1.5	7.6	b
Mn^{2+}	1.6	0.1	31.2	2.7	1.5	b	21.6	1.0	1.7	a	4.5	0.6	0.9	c
Na^{+}	50.2	—	2.0	0.2	—		10.3	1.0	—		—	—	—	
NH_4^{+}	8.5	0.3	6.4	0.7	0.3	c	15.4	0.8	1.2	b	7.6	0.3	1.5	a
Zn^{2+}	0.2	0.01	0.3	0.02	0.01	b	0.2	0.03	0.02	ab	0.1	0.01	0.03	a
NO_3^{-}	4.3	40.1	2.5	0.1	34.4	a	2.5	0.3	25.7	b	1.3	<0.1	35.8	a
HPO_4^{2-}	6.5	59.9	4.7	0.1	65.6	b	7.2	0.3	74.1	a	2.4	0.1	64.2	b
SO_4^{2-}	—	—	12.4	0.9	—		9.9	0.3	—		4.2	0.2	—	
Total cations	3050		207				1310				—			
Total anions	—		19.6				19.6				7.9			

(*continued*)

Table 3. Continued.

			Resin capsule counterions											
	Chemical		HCl				HOH				$NaHCO_3$			
Nutrient	Mean	%	Mean	SE	%		Mean	SE	%		Mean	SE	%	
e. Site 5														
Ca^{2+}	2700	90.2	1790	94.6	83.6	a	751	40.0	80.0	b	391	25.4	80.1	b
Cu^{2+}	0.4	0.01	0.9	0.03	0.041	c	0.5	0.02	0.050	b	0.3	0.01	0.055	a
Fe^{2+}	9.0	0.3	8.4	0.8	0.4	ab	2.7	0.1	0.3	b	2.8	0.1	0.6	a
K^{+}	189	6.3	80.2	1.5	3.8	b	68.9	1.6	7.4	ab	44.8	3.8	9.2	a
Mg^{2+}	86.3	2.9	215	12.9	10.0	a	83.3	6.3	8.9	b	36.9	2.4	7.6	c
Mn^{2+}	2.4	0.1	38.3	2.0	1.8	a	17.1	3.3	1.8	a	2.2	0.2	0.5	b
Na^{+}	51.7	—	10.4	0.2	—		11.9	0.3	—		—	—	—	
NH_4^{+}	5.1	0.2	6.2	0.3	0.3	c	14.7	0.6	1.6	b	9.8	0.6	2.0	a
Zn^{2+}	0.2	0.01	0.3	0.01	0.014	c	0.2	<0.01	0.018	b	0.1	0.01	0.024	a
NO_3^{-}	0.3	3.4	2.7	0.3	36.0	NS	3.3	0.7	37.8	NS	1.7	0.3	40.4	NS
HPO_4^{2-}	9.0	96.6	4.7	<0.1	64.1	NS	5.3	0.4	62.2	NS	2.4	0.1	59.6	NS
SO_4^{2-}	—	—	13.0	0.7	—		7.9	0.1	—		4.4	0.2	—	
Total cations	3040		2150				950				—			
Total anions	—		20.4				16.4				8.5			

averages were generally greater with H^+-resin extraction, the latter more with HOH- than HCl-resins. In soils from Sites 2–5, HCl-extracted Fe^{2+} was greater than that extracted with the other two forms ($F = 21.0$; $p < 0.001$) and HOH-extracted Na^+ exceeded HCl-extracted Na^+ ($F = 14.5$; $p < 0.001$). NH_4^+ was extracted in the greatest net quantities with HOH-resins in soils from Sites 2, 4, and 5 ($F = 31.8$; $p < 0.001$). NO_3^- patterns were inconsistent among sites, and no nutrient at any site desorbed in greatest net quantities from $NaHCO_3$-resins.

Relative to resin measurements, chemical extraction yielded high proportional K^+ except from Site 5 soils, and low Cu^{2+}, Mg^{2+}, and Mn^{2+} (Table 3a–e). Of all of the nutrients measured, chemical representation of proportional Ca^{2+} and Zn^{2+} was the most similar to the resin methods.

HCl-resins extracted proportionally more Cu^{2+} than chemical extraction, but less than the other resins. Except for soils from Site 3, HCl-resins extracted low proportional K^+. Except for soils from Site 5, HOH-resins extracted high proportional HPO_4^{2-} and low proportional NO_3^- relative to other resins. $NaHCO_3$-resins extracted relatively high proportions of Cu^{2+}, Fe^{2+} (except at Site 1), and Zn^{2+} (except at Site 3), and low Mn^{2+} relative to other resins. The representation of soil Na^+ on $NaHCO_3$-charged resins is unknown, but this cation represented an average of 1.8, 0.3, and 0.9 of all cations extracted by chemical means, HCl-resins, and HOH-resins, respectively.

Due to the relatively large number of nutrients compared among methods, we ranked nutrients in order of their net extraction within each site (Table 4) to offer a clearer picture of the data. All methods in all soils extracted Ca^{2+} in the greatest quantities (range 82.3–93.3%) and Zn^{2+} in the least (range 0.01–0.03%). K^+ was second-most abundant in all soils using chemical techniques (range 4.1–9.5%), and Mg^{2+} was second-most abundant in all resin analyses (range 4.6–10.3%) except by $NaHCO_3$-resins in Site 5 soils. Anions were extracted in the order $SO_4^{2-} > HPO_4^{2-} > NO_3^-$ by all analyses. As suggested by the proportional comparisons, and with the exception of $NaHCO_3$ extraction of Mn^{2+} from Site 5 soils, Mg^{2+} and Mn^{2+} ranked lower with chemical extraction (ranges 1.9–4.0%, Mg^{2+}; < 0.1–0.1, Mn^{2+}) than resin methods (ranges 4.6–10.3%, Mg^{2+}; 0.4–1.9, Mn^{2+}). In all soils, Fe^{2+} ranked relatively low with HOH-resin extraction, as did SO_4^{2-} except in Site 3 soils where the HOH-SO_4^{2-} ranking matched that of $NaHCO_3$. Similarly, in all soils, NH_4^+ ranked low with HCl-resin extraction, as did Na^+ except at Site 5 where HCl-Na^+ ranking matched that of HOH. Na^+ and HPO_4^{2-} ranked high with chemical extraction, except for HPO_4^{2-} in Site 3 soils. Mn^{2+} extraction ranked relatively high with both HCl- and HOH-resins.

We also ranked the CNP sites specific to nutrient and extraction method (Table 5) for greater clarity in interpreting the data. This ranking also shows

Table 4. Descending order of inorganic nutrients measured by chemical and resin extractions. Data are separated by site, indirectly accounting for site × counterion interactions. Ranks are based on μmol_c. Na^+ data for $NaHCO_3$-charged resins are disregarded and SO_4^{2-} data for chemical extractions are unavailable.

Site	Method		Order of representation											
1	Chemical extraction		Ca	K	Mg	Na	NH_4	HPO_4	Mn	Fe	Cu	NO_3	Zn	
	Resin counterions:	HCl	Ca	Mg	Mn	K	SO_4	Fe	Na	NH_4	HPO_4	NO_3	Cu	Zn
		HOH	Ca	Mg	K	Mn	NH_4	Na	SO_4	HPO_4	Fe	NO_3	Cu	Zn
		$NaHCO_3$	Ca	Mg	K	Fe	SO_4	Mn	NH_4	HPO_4	NO_3	Cu	Zn	
2	Chemical extraction		Ca	K	Mg	Na	NH_4	HPO_4	Fe	Mn	NO_3	Cu	Zn	
	Resin counterions:	HCl	Ca	Mg	K	Mn	SO_4	Fe	NH_4	HPO_4	Na	NO_3	Cu	Zn
		HOH	Ca	Mg	K	Mn	NH_4	Na	SO_4	HPO_4	Fe	NO_3	Cu	Zn
		$NaHCO_3$	Ca	Mg	K	NH_4	SO_4	Fe	Mn	HPO_4	NO_3	Cu	Zn	
3	Chemical extraction		Ca	K	Na	Mg	NH_4	Fe	HPO_4	NO_3	Mn	Cu	Zn	
	Resin counterions:	HCl	Ca	Mg	K	Mn	SO_4	NH_4	Fe	Na	HPO_4	NO_3	Cu	Zn
		HOH	Ca	Mg	K	Mn	NH_4	SO_4	Na	HPO_4	Fe	NO_3	Cu	Zn
		$NaHCO_3$	Ca	Mg	K	Fe	NH_4	SO_4	HPO_4	Mn	NO_3	Cu	Zn	
4	Chemical extraction		Ca	K	Mg	Na	NH_4	HPO_4	NO_3	Fe ≡	Mn	Cu	Zn	
	Resin counterions:	HCl	Ca	Mg	K	Mn	SO_4	Fe	NH_4	HPO_4	NO_3	Na	Cu	Zn
		HOH	Ca	Mg	K	Mn	NH_4	Na	SO_4	HPO_4	Fe	NO_3	Cu	Zn
		$NaHCO_3$	Ca	Mg	K	NH_4	Mn	SO_4	Fe	HPO_4	NO_3	Cu	Zn	
5	Chemical extraction		Ca	K	Mg	Na	HPO_4 ≡	Fe	NH_4	Mn	Cu	NO_3	Zn	
	Resin counterions:	HCl	Ca	Mg	K	Mn	SO_4	Na	Fe	NH_4	HPO_4	NO_3	Cu	Zn
		HOH	Ca	Mg	K	Mn	NH_4	Na	SO_4	HPO_4	NO_3	Fe	Cu	Zn
		$NaHCO_3$	Ca	K	Mg	NH_4	SO_4	Fe	HPO_4	Mn	NO_3	Cu	Zn	

Table 5. Ranking of sites according to μmol_c nutrients extracted by each method. A rank of 1 indicates that that site yielded the most nutrient quantity specific to the indicated method. Average deviations from the mean ranking are absolute (not standard). Na^+ data for $NaHCO_3$-charged resins are disregarded and SO_4^{2-} data for chemical extractions are unavailable.

		Rank (descending)								Rank (descending)					
Nutrient	Method	Site 1	Site 2	Site 3	Site 4	Site 5	Sum	Nutrient	Method	Site 1	Site 2	Site 3	Site 4	Site 5	Sum
Ca^{2+}	Chemical	1	4	5	2	3		Na^+	Chemical	2	3	1	5	4	
	HCl	2	3	1	4	5			HCl	2	4	3	5	1	
	HOH	4	1	3	2	5			HOH	4	2	5	3	1	
	$NaHCO_3$	4	1	3	2	5									
	Avg. dev., resins only	0.89	0.89	0.89	0.89	0.00	3.56		Avg. dev., resins only	1.00	1.00	1.00	1.00	0.00	4.00
	Avg. dev., all methods	1.25	1.25	1.00	0.75	0.75	5.00		Avg. dev., all methods	0.89	0.67	1.33	0.89	1.33	5.11
Cu^{2+}	Chemical	1	3	3	2	2		NH_4^+	Chemical	2	1	3	4	5	
	HCl	1	2	2	2	1			HCl	5	3	1	2	4	
	HOH	2	1	2	1	2			HOH	4	3	5	1	2	
	$NaHCO_3$	1	2	3	2	2			$NaHCO_3$	5	3	4	2	1	
	Avg. dev., resins only	0.44	0.44	0.44	0.44	0.44	2.22		Avg. dev., resins only	0.44	0.00	1.56	0.44	1.11	3.56

(*continued*)

Table 5. Continued.

Nutrient	Method	Rank (descending) Site 1	Site 2	Site 3	Site 4	Site 5	Sum	Nutrient	Method	Rank (descending) Site 1	Site 2	Site 3	Site 4	Site 5	Sum
	Avg. dev., all methods	0.38	0.50	0.50	0.38	0.38	2.13		Avg. dev., all methods	1.00	0.75	1.25	0.88	1.50	5.38
Fe^{2+}	Chemical	5	3	2	4	1		Zn^{2+}	Chemical	1	1	1	1	1	
	HCl	2	4	3	5	1			HCl	2	2	1	2	2	
	HOH	1	3	4	2	5			HOH	1	1	1	1	1	
	$NaHCO_3$	1	2	3	4	5			$NaHCO_3$	1	1	2	2	2	
	Avg. dev., resins only	0.44	0.67	0.44	1.11	1.78	4.44		Avg. dev., resins only	0.44	0.44	0.44	0.44	0.44	2.22
	Avg. dev., all methods	1.38	0.50	0.50	0.88	2.00	5.25		Avg. dev., all methods	0.38	0.38	0.38	0.50	0.50	2.13
K^+	Chemical	1	4	5	3	2		NO_3^-	Chemical	4	3	2	1	5	
	HCl	4	2	5	3	1			HCl	4	1	5	3	2	
	HOH	2	3	5	4	1			HOH	3	4	4	2	1	
	$NaHCO_3$	2	3	5	4	1			$NaHCO_3$	3	4	5	2	1	
	Avg. dev., resins only	0.89	0.44	0.00	0.44	0.00	1.78		Avg. dev., resins only	0.44	1.33	0.44	0.44	0.44	3.11

	Avg. dev., all methods	0.88	0.50	0.00	0.50	0.38	2.25		Avg. dev., all methods	0.50	1.00	1.00	0.50	1.38	4.38
Mg^{2+}	Chemical	1	4	5	2	3		HPO_4^{2-}	Chemical	4	2	3	5	1	
	HCl	2	4	5	3	1			HCl	1	3	4	2	2	
	HOH	2	3	5	1	4			HOH	2	3	5	1	4	
	$NaHCO_3$	1	2	5	3	4			$NaHCO_3$	1	2	4	3	3	
	Avg. dev., resins only	0.44	0.67	0.00	0.89	1.33	3.33		Avg. dev., resins only	0.44	0.44	0.44	0.67	0.67	2.67
	Avg. dev., all methods	0.50	0.75	0.00	0.75	1.00	3.00		Avg. dev., all methods	1.00	0.50	0.50	1.25	1.00	4.25
Mn^{2+}	Chemical	1	4	5	3	2		SO_4^{2+}	HCl	3	1	2	4	2	
	HCl	2	4	5	3	1			HOH	4	1	3	2	5	
	HOH	3	1	5	2	4			$NaHCO_3$	1	2	5	4	3	
	$NaHCO_3$	2	3	5	1	4									
	Avg. dev., resins only	0.44	1.11	0.00	0.67	1.33	3.56		Avg. dev., resins only	1.11	0.44	1.11	0.89	1.11	4.67
	Avg. dev., all methods	0.50	1.0	0.00	0.75	1.25	3.50								

inconsistencies among methods. HOH- and $NaHCO_3$-resins appear to share the most similarities, but this agreement is not consistent among all nutrients. Chemical extraction of carbonate-related nutrients Ca^{2+}, Cu^{2+}, Mg^{2+}, and Mn^{2+} followed roughly similar patterns; K^+ also conformed to this among-site pattern. Importantly, in examining the most abundant nutrients (from Table 4), variation in the site ranking among methods is greater for carbonate-related Ca^{2+} and Mg^{2+} than for the non-carbonate related K^+ (Table 5).

DISCUSSION

Among five CNP soils, different nutrient extraction techniques yielded disparities in net quantities, ionic proportions, and abundance rankings of nutrients (Tables 2–5), indicating that the methods are not comparable. Importantly, which of the methods most closely represents actual plant-available nutrient levels is unknown and is certainly dependent on the characteristics of the local ecosystem. The soils used for this study were from Canyonlands National Park, a site with highly calcareous soils that are sensitive to fluctuations in moisture, temperature, and pH[1,16,22] that can be induced by various extraction techniques. The following discussion is in the context of the particular environmental conditions of CNP, but the implications of this study emphasize the universal importance of understanding the differential effects of alternate methods on soil chemistry.

H^+-containing resins, particularly HCl-resins, adsorbed more total soil cations and anions than did Na^+-containing resins (Table 3a–e). The especially low affinity of resins for H^+[4] may explain the generally greater cation extraction with HCl- and HOH-resins, but it does not explain discrepancies in net nutrient sorption between HCl- and HOH-resins, found for Ca^{2+}, Cu^{2+}, Fe^{2+}, Mg^{2+}, Mn^{2+}, Na^+, HPO_4^{2-}, and SO_4^{2-}. Because the only difference between these two counterion combinations was the associated anion, different nutrient extraction patterns between HCl- and HOH-resins may be attributable to differences in Cl^- and OH^- dynamics.

Cl^- is less likely than OH^- to influence cation adsorption because OH^- has a greater capacity to affect pH and biogeochemical reactions. Many commonly used counterions, such as H^+, HCO_3^- and OH^-, can affect pH in the vicinity of the resins, which will in turn influence the solubility and/or soil release of certain elements.[1,4,7] In the pH range of the soils tested for this comparison (Table 1), resin release of OH^- induces more alkaline conditions in the resin environment and in turn should decrease the resin sorption of HPO_4^{2-}[7,28] and other carbonate-related cations such as Ca^{2+}, Cu^{2+}, Mg^{2+}, and Mn^{2+}. There are counteracting processes in a mixed-bed system such as

ours, however, as simultaneous H^+ desorption can acidify the resin environment and actually promote the solubility of carbonate-related cations.[1] The pH buffer capacity of the soils used in this comparison (% $CaCO_3$ equiv. in Table 1) was not so high that it would preclude these reactions.[4] Because Cl^- does not have the same effect on solution pH as OH^-, we conclude that net acidification in the vicinity of the HCl-charged resin was largely responsible for greater solubility and subsequent adsorption of Ca^{2+}, Cu^{2+}, Fe^{2+}, Mg^{2+}, Mn^{2+}, and SO_4^{2-} from most of the soils by HCl-loaded resins. HOH-resin extraction of HPO_4^{2-} may be greater than HCl-resin extraction because resin affinity for Cl^- is greater than that for OH^-[4] and OH^-/HPO_4^{2-} exchange is consequently easier. The reasons for greater extraction of Na^+ and NH_4^+ by HOH-resins remain unclear; one possibility is that HCl effected greater dissolution of $CaCO_3$ and the solubilized Ca^{2+}, which is a high-affinity ion,[4] competitively displaced Na^+ and NH_4^+ from HCl-resin exchange sites.

Resin counteranions could also affect cation adsorption in other ways. Exchange of HCO_3^-, for example, could result in precipitation of carbonate-associated ions[16] and reduce adsorption of Ca^{2+}, Cu^{2+}, Mg^{2+}, Mn^{2+}, HPO_4^{2-}, and Zn^{2+} on $NaHCO_3$-resins. As a buffer, however, HCO_3^- desorption may also have the opposite effect and solubilize carbonates through a pH decrease, particularly in high-pH soils.[15] Desorption of OH^- from HOH-resins, via reactions with CO_2 ($\rightarrow HCO_3^-$), could have similar effects. This phenomenon could have indirect effects on other ions; for example, higher average HPO_4^{2-} sorption on HOH-resins could decrease that of SO_4^{2-}, as shown by their extraction data between HCl- and HOH-resins in all soils but those from Site 3 (Table 3a–e).

Because many of our field studies at CNP concern soil P status and dynamics,[23,29] this nutrient was of especial interest in these method comparisons. In all soils except for those from Site 5, our data show greatest proportional extraction of HPO_4^{2-} with OH^- (Table 3a–e), accountable by the greater resin affinity for Cl^- and HCO_3^- than for OH^-.[4,15] With the exception of Site 2 data, our results generally corroborate the anion-exchange resin bead studies of Bache and Ireland,[16] who found little difference between HCO_3^- and Cl^- as HPO_4^{2-} counteranions in a calcareous soil (pH 7.5), but are in contrast to the study of Sibbesen,[15] who found that HCO_3^- extracted more HPO_4^{2-} than Cl^-, also in a calcareous soil (pH 7.3).

We detected some consistent patterns among soils with respect to a method's preferential extraction of certain nutrients, such as proportionally lower extraction of Cu^{2+}, Mg^{2+}, and Mn^{2+} with chemical methods (Table 3a–e). Mg^{2+} was extracted with NH_4OAc, which operates on the principle of cationic exchange between NH_4^+ and the target cations from soil exchange

sites. The theory that affinity for a soil exchange site occurs in the order $NH_4^+ > Na^+ \approx H^+$[30] would predict higher proportional values of all nutrients extracted with NH_4OAc, i.e., Ca^{2+}, K^+, Mg^{2+}, and Na^+. Proportional Ca^{2+}, K^+, and Na^+ indeed were relatively high by chemical extraction in most soils (exceptions are Site 1 for Ca^{2+} and Site 5 for K^+), but proportional Mg^{2+} was noticeably lower (Table 3a–e), the reasons for which are unexplained. With respect to Ca^{2+}, it also is possible that the NH_4OAc extraction, even at pH 8.5,[24] dissolves some fine-grained $CaCO_3$ concretions, resulting in an erroneously high estimate of exchangeable Ca^{2+}. Either of these mechanisms should be taken into account when considering NH_4OAc extraction, particularly in high-carbonate soils.

Proportional Cu^{2+} and Mn^{2+}, also carbonate-related nutrients, were determined to be lower with chemical DTPA extraction, a procedure that also uses $CaCl_2$ to minimize the dissolution of carbonates.[31] In theory, the $CaCl_2$ may affect carbonate-related nutrients the least of the four options that we examined. The sensitivity of carbonates to biogeochemical alteration is difficult to gage with measures of Cu^{2+} and Mn^{2+}, however, as the opposing effects of carbonate dissolution by resin-H^+ and precipitation by resin-OH^- and resin-HCO_3^- are not evident in Table 3.

The inconsistent nutrient patterns among methods when compared from soil to soil (Table 3a–e) strongly suggest that the most appropriate method is specific to soil type. In calcareous soils such as CNP with substantial levels of carbonates and carbonate-related nutrients, we assert that a nutrient extraction technique that biogeochemically alters soil carbonates is inappropriate for measuring plant-available nutrients. Such alteration might occur with NH_4OAc- or H^+-induced dissolution of carbonates, or OH^- or HCO_3^--induced precipitation of the same. These analyses suggest that pH manipulation results in greater adsorption of several nutrients by HCl-resins, but that nutrient representation may also be affected by differing ion-resin affinities and interactions among ions. It is proposed that it is necessary to identify the nutrients of foremost interest to a study and to understand differences in their resin sorption and conventional chemical extraction dynamics in selecting a method of measurement. Studies of soil nutrient bioavailability should determine which method is most appropriate for particular soils and particular species or functional types.

Many extractions are conducted to determine the quantities of plant-available nutrients. It is difficult, however, to compare the ion affinities of resins with those of plant roots, to determine whether resin desorption of H^+ replicates that of plant roots, and whether this is in proportion to other ions sorbed. Because we do not know how accurately extraction methods represent biological uptake of any single nutrient, we also do not know the "best"

method to determine these quantities. Our study highlights the fact that various techniques for measuring soil nutrients with ion-exchange resins have differential effects on the soil-resin environment and yield data that should not be compared nor considered interchangeable. Studies of soil nutrient bioavailability should determine which methods are most appropriate for the particular soils, plant species and/or functional types of interest.

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Repeated Use of Ion-Exchange Resin Membranes in Calcareous Soils

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ABSTRACT

This study compared the consistency of nutrient extraction among repeated cycles of ion-exchange resin membrane use. Two sandy calcareous soils and different equilibration temperatures were tested. No single nutrient retained consistent values from cycle to cycle in all treatments, although both soil source and temperature conferred some influence. It was concluded that the most conservative use of resin membranes is single-use.

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INTRODUCTION

Ion-exchange resins, used for over 40 years,[1] have been demonstrated to be effective measures of soil nutrients in both terrestrial and aquatic ecosystems.[2–4] Among different forms of ion-exchange resins such as bags, capsules, and membranes, only membranes are considered to be reusable because they do not have an encasing mesh like that of bags and capsules, which can trap soil particles and fine roots and result in questionable data.[5] However, it has also been stated that because ion desorption from resins is never complete,[6,7] no resins should be reused. The objective was to determine the integrity of data with repeated use of ion-exchange resin membranes. This study tested for differences in ion-exchange resin membrane performance in soils from two sources and at different equilibration temperatures.

MATERIALS AND METHODS

Cation-exchange membranes (CEMs; CR 67, Dynambio, Madison, WI) were cut to 3.5 × 5 cm and charged with H^+ by placing them in 0.2 *M* HCl for 2 h with the solution replaced halfway through the equilibration period. Anion-exchange membranes (AEMs; AR 204, Dynambio) were charged, also 3.5 × 5 cm, with OH^- in the same manner using 0.5 *M* NaOH. Soils were collected from two sites within the Needles District of the Canyonlands National Park in southeast Utah (38.17°N, 109.98°W), an arid ecosystem averaging 214 mm annual precipitation (1965–1997) and 11.6°C.[8] Soils were Typic Calciorthids from the Nakai series ("Nakai" soils) and Typic Torripsamments from the Sheppard series ("Sheppard" soils; USDA Soil Taxonomy). Soils were sieved (2 mm) and mixed with enough deionized (DI) water to make a saturated paste.[9] Within the saturated pastes of each soil type, we embedded 10 replicates of CEM–AEM pairs and covered the cups with plastic wrap. Five replicates of each soil were placed in a cold frame and five were placed in a seedling propagator room at the Denver Botanic Gardens (Denver, CO) for the cold and warm treatments, respectively (Table 1). Samples equilibrated for one week, at the end of which all membranes were removed, rinsed thoroughly with DI water, and stored at 0°C. At the Soil and Plant Analysis Laboratory at Brigham Young University, all ions were desorbed from resin membranes in 2 *M* HCl for 1 h and all but inorganic N were measured by inductively coupled plasma spectrometry. Ammonium (NH_4^+) and nitrate (NO_3^-) were determined by titration with H_2SO_4. Results were reported in μg membrane^{-1} and converted to μmol$_c$ membrane^{-1}.

Table 1. Equilibration temperatures for repeated resin membrane comparisons at either the Denver Botanic Gardens (DBG) or the University of Denver (DU).

Trial and month (2000)	Treatment	Location	Avg. max (°C)	Avg. min. (°C)
(1) February	Warm	Greenhouse, DBG	34	18
	Cold	Cold frame, DBG	23	−4
(2) July	Warm	Greenhouse, DU	33	21
	Cold	Refrigerator, DU	10	0
(3) September	Warm	Greenhouse, DU	31	19
	Cold	Refrigerator, DU	−2	−1

After desorption, membranes were recharged by the same methods that they were originally charged. The above methods were repeated twice more, for which the membranes were randomly placed in saturated pastes that varied by soil type and equilibration temperature (Table 1). Resins were not frozen in these latter two trials. Nutrients were extracted as described above.

The Na^+ was disregarded from the membrane data due to initial AEM charging with NaOH. Multivariate ANOVA was performed on nutrient data with trial, temperature, and soil source as factors. The nutrients were also ranked from most to least abundant as another means of comparison between cycles of membrane use.

RESULTS

There were significant differences among trials and between equilibration temperature and soil source for most nutrients (Table 2). Interactions among factors were also apparent; for example, there were more significant differences overall between trials in Nakai soils equilibrating in cold temperatures than in warm temperatures (Table 3a), and the opposite was true for Sheppard soils (Table 3b).

In both soils, Ca^{2+} and Mg^{2+} retained comparable values among trials under cold conditions, but increased between Trials 2 and 3 under warm conditions (Table 3). Although differences were not always significant, average Cu^{2+} values generally increased between Trials 1 and 2 and always significantly decreased between Trials 2 and 3. The only condition under which Mn^{2+} showed significant differences was with warm equilibration in Sheppard soils. No nutrient retained comparable values when results from all treatments, trials, and soils were compared. There was also no pattern to

Table 2. F values of MANOVA comparing the amounts of nutrients extracted by ion-exchange resin membranes in repeated trials that varied by soil source and equilibration temperature.

Nutrient	Trial		Temperature		Soil Source		Trial × Temperature		Trial × Soil Source		Temperature × Soil Source		Trial × Temp × Soil Source	
Ca^{2+}	11.2	***	26.3	***	56.3	***	21.0	***	0.5		0.2		0.1	
Cu^{2+}	73.8	***	0.1		0.2		1.4		6.2	**	4.5	*	2.4	
Fe^{2+}	89.9	***	82.1	***	3.3		7.6	**	32.4	***	2.1		11.4	***
K^{+}	82.7	***	14.3	***	714.1	***	42.0	***	15.8	***	21.9	***	13.0	***
Mg^{2+}	3.2		105.6	***	2538.2	***	20.0	***	1.7		34.3	***	7.3	**
Mn^{2+}	17.2	***	129.3	***	4.1	*	18.7	***	5.9	**	0.2		7.2	**
NH_4^{+}	35.7	***	3.5		0.9		0.1		1.4		0.2		1.2	
NO_3^{-}	7.2	**	49.7	***	21.9	***	0.6		0.1		5.8	*	0.8	
HPO_4^{2-}	55.6	***	13.8	**	670.5	***	10.5	***	43.2	***	1.5		2.8	
SO_4^{2-}	6.5	**	86.3	***	18.3	***	34.9	***	12.5	***	10.0	**	1.1	
Zn^{2+}	25.9	***	7.3	*	5.9	*	10.8	***	14.5	***	2.9		6.0	**

$*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Table 3. Mean and SE of nutrients desorbed from resin membranes in repeatability trials (μmol_c membrane^{-1}). Asterisks indicate significant differences between trials within temperature treatments.

	Cold								Warm							
	Trial 1			Trial 2			Trial 3		Trial 1			Trial 2			Trial 3	
Nutrient	Mean	SE		Mean	SE		Mean	SE	Mean	SE		Mean	SE		Mean	SE
(a) Nakai soils																
Ca^{2+}	931.2	19.6		899.6	29.3		869.6	44.0	925.5	21.4		952.7	16.6	**	1158.5	55.9
Cu^{2+}	0.12	<0.01	*	0.21	0.03	**	0.03	0.01	0.11	0.01		0.16	0.02	**	0.04	0.01
Fe^{2+}	3.9	0.5		3.2	0.3	***	1.0	0.1	7.4	0.5	**	3.3	0.6		1.9	0.2
K^{+}	9.5	0.3	***	5.4	0.1		5.8	0.5	7.8	0.1		6.9	0.5	**	10.8	0.7
Mg^{2+}	202.5	4.8		184.7	5.8		173.8	10.7	220.8	4.0		225.7	2.9	**	270.3	12.7
Mn^{2+}	0.9	0.1		0.9	0.1		1.1	0.1	5.8	0.1		3.5	0.9		1.3	0.4
NH_4^{+}	6.6	0.6	***	1.5	0.6	**	4.4	0.3	6.8	0.7		3.5	1.2		5.3	1.0
NO_3^{-}	2.4	0.3		2.0	0.3		2.7	0.5	0.4	0.1		0.7	0.3		1.5	0.4
HPO_4^{2-}	2.2	0.1	*	1.7	0.1	***	0.8	0.1	2.0	0.1		1.7	0.1	*	1.3	0.1
SO_4^{2-}	9.3	0.2		8.7	0.2	**	6.7	0.3	10.2	0.2		9.8	0.3		10.6	0.5
Zn^{2+}	0.14	0.01	**	0.30	0.04	**	0.13	0.01	0.19	0.01		0.23	0.02		0.18	0.02
(b) Sheppard soils																
Ca^{2+}	1096.1	55.3		1044.7	20.2		1039.9	34.0	1082.2	14.7		1057.2	34.9	**	1327.7	45.0
Cu^{2+}	0.13	0.01		0.13	0.01	***	0.05	0.01	0.12	0.01	**	0.17	0.01	***	0.08	0.01
Fe^{2+}	2.9	0.1	**	3.9	0.3	***	1.5	0.1	5.0	0.3	**	7.2	0.2	***	2.5	0.2
K^{+}	5.4	0.2	***	1.2	0.1		1.4	0.2	4.1	0.2	***	1.3	0.1	**	2.1	0.1
Mg^{2+}	48.6	2.7		43.0	1.5		39.4	3.2	54.1	0.8		55.1	0.6	**	64.5	1.9
Mn^{2+}	0.7	0.1		0.6	<0.1		0.6	0.1	3.1	0.1	***	4.3	0.1	***	1.6	0.5
NH_4^{+}	7.5	0.7	**	3.2	1.0		3.6	0.8	8.5	0.2	***	2.9	0.8		4.9	0.6
NO_3^{-}	1.1	0.4		0.9	0.1		1.7	0.1	0.4	0.1		0.4	0.1	*	0.8	0.1
HPO_4^{2-}	0.45	0.03		0.48	0.01	**	0.29	0.04	0.56	0.01	**	0.65	0.01		0.63	0.03
SO_4^{2-}	8.8	0.4	*	7.8	0.1		7.7	0.2	8.7	0.1	**	8.0	0.1	***	10.4	0.3
Zn^{2+}	0.15	0.01		0.17	<0.01	**	0.13	0.01	0.26	0.02	*	0.19	0.01	**	0.13	0.01

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 4. Descending order of inorganic nutrients measured by chemical and resin extractions. Ranks are based on μmol_c.

Soil	Temp.	Trial	Order of representation									
Nakai series	Cold	(1)	Ca	Mg	K	SO_4	NH_4	Fe	NO_3	HPO_4	Mn	Zn	Cu
		(2)	Ca	Mg	SO_4	K	Fe	NO_3	HPO_4	NH_4	Mn	Zn	Cu
		(3)	Ca	Mg	SO_4	K	NH_4	NO_3	Mn	Fe	HPO_4	Zn	Cu
	Warm	(1)	Ca	Mg	SO_4	K	Fe	NH_4	Mn	HPO_4	NO_3	Zn	Cu
		(2)	Ca	Mg	SO_4	K	Mn	NH_4	Fe	HPO_4	NO_3	Zn	Cu
		(3)	Ca	Mg	K	SO_4	NH_4	Fe	NO_3	HPO_4	Mn	Zn	Cu
Sheppard series	Cold	(1)	Ca	Mg	SO_4	NH_4	K	Fe	NO_3	Mn	HPO_4	Zn	Cu
		(2)	Ca	Mg	SO_4	Fe	NH_4	K	NO_3	Mn	HPO_4	Zn	Cu
		(3)	Ca	Mg	SO_4	NH_4	NO_3	Fe	K	Mn	HPO_4	Zn	Cu
	Warm	(1)	Ca	Mg	SO_4	NH_4	Fe	K	Mn	HPO_4	NO_3	Zn	Cu
		(2)	Ca	Mg	SO_4	Fe	Mn	NH_4	K	HPO_4	NO_3	Zn	Cu
		(3)	Ca	Mg	SO_4	NH_4	Fe	K	Mn	NO_3	HPO_4	Zn	Cu

nutrient values obtained from repeated use of the membranes. For example, extraction of some nutrients under some conditions increased with the 2nd use of the membrane and then decreased with the 3rd use (Fe^{2+}, Cu^{2+}, Mn^{2+}, SO_4^{2-}).

All cycles of membrane use in all treatments identified Ca^{2+} and Mg^{2+} as the first and second most abundant nutrients, respectively, and all identified Zn^{2+} and Cu^{2+} as the least abundant (Table 4). The K^+ and SO_4^{2-} were alternately ranked as the 3rd- and 4th-most available nutrients in Nakai soils, while SO_4^{2-} was consistently identified as the 3rd-most abundant nutrient in all data from Sheppard soils. The variation in ranking of all the other nutrients was specific to soil source and equilibration temperature.

DISCUSSION

Repeated use of ion-exchange membranes in these sandy calcareous soils resulted in inconsistent measures of all nutrients among cycles in at least one treatment (Table 3). Moreover, variation in the ranking of nutrients by abundance was detectable at levels of the 3rd-most abundant nutrient for Nakai soils and 4th-most abundant for Sheppard soils (Table 4). In contrast to our observations, the manufacturer of resin membranes claims that resins can be reused 5–20 times,[10] and other researchers have reused membranes between 3 and 500 times without any decline in performance.[5,11,12]

One methodological difference between trials was that resins were frozen after Trial 1, but not after Trials 2 or 3. This inconsistency could have affected results between the first two trials but does not account for differences between the second two. In fact, significant differences were more frequently shown between the 2nd and 3rd trials than between the first two (Table 3). Increases in resin adsorption between trials, such as observed with Ca^{2+} under warm conditions, could be due to ion buildup in resin interspaces that desorbed more effectively in subsequent elution steps (W. Jarrell, personal communication). Because our elution procedures were identical throughout, this seems improbable. Normal resin degradation could account for less effective sorption of other nutrients, but this was not expected after a single use. It was concluded that the most conservative use of resin membranes was single-use.

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Section II: What site factors confer resistance to invasion by *Bromus*? Is it soil chemistry, microhabitat, or less herbivory? Can these factors also predict areas susceptible to invasion by *Bromus* and other exotic annual grasses on a landscape and regional scale?

Several factors can determine the success of vascular plants. These include microhabitat conditions, herbivory, and soil chemistry. Microhabitat can alter plant germination, growth, and survival by modifying light, water, nutrients and herbivore damage. Herbivory can directly impact plant success, and soil chemistry can determine plant performance. Soil chemistry may determine invasion patterns. In Canyonlands National Park, the annual invasive grass *Bromus* generally occurs in areas dominated by *Hilaria* and rarely in areas dominated by *Stipa*. To determine if the success of *Bromus* in *Hilaria* patches was determined by the microhabitat created by *Hilaria*, we examined the effects of plant canopy, plant litter and herbivory on the emergence, growth and survival of *Bromus*. In a field experiment we planted *Bromus* either under the canopy of *Hilaria* or *Stipa* or in the interspace, with and without *Hilaria* litter, and with and without rodent herbivory. We also reciprocally transplanted soils, moving soils from a *Stipa*-dominated area into a *Hilaria* area and vice versa so that soils varied but microhabitats did not. These experiments were conducted in an extreme drought year and an almost average year. *Bromus* emergence and biomass was similar in *Hilaria*-dominated and *Stipa*-dominated sites for all treatments. Being under a plant canopy increased emergence in the drought year, but did not affect emergence in the almost average year. In contrast, plant canopy had negative effects on biomass and survival of *Bromus*. Herbivory negatively affected emergence only in the drought year but had no effect on biomass and decreased survival in both years. *Hilaria* litter increased *Bromus* emergence, did not affect biomass, and decreased survival. Our results support other studies that show facilitative and competitive interactions may change throughout a plant's life cycle and depend on abiotic conditions. Although we found several microhabitat factors to influence *Bromus*, these factors did not differ between patches of *Hilaria* and *Stipa*. This suggests that although these factors influenced *Bromus* success, they did not explain the observed association between *Bromus* and *Hilaria*. We suggest this supports our previous contention that *Bromus* invasion into *Hilaria* areas is explained by soil chemistry.

Based on our observation that the invasion of annual grass appears controlled by soil chemistry, we investigated the effect of site factors on annual grass cover in 432 sites in the Chihuahuan, Mojave, Colorado Plateau, and Great Basin deserts. At these sites, we assessed plant cover, ground cover, slope, aspect, elevation, and soil chemistry. Our results show that soil chemistry defines the difference between uninvaded and invaded patches in most instances. Invaded patches in regions with lower winter precipitation had higher available phosphorus than uninvaded patches. As winter precipitation increased, the importance of phosphorus declined and the importance of available potassium increased. Soil depth was important in areas with shallow soils, and texture played a role in some cases. Because soil texture and nutrients are mappable, annual plant invasions should also be mappable. Site factors that confer resistance to invasion can also be used to design soil amendments to suppress annual grass invasions.

What site factors confer resistance to invasion by *Bromus*? Is it soil chemistry, microhabitat, or less herbivory? Can these factors also predict areas susceptible to invasion by *Bromus* and other exotic annual grasses on a landscape and regional scale?

- Resistance to invasion was not determined by microhabitat or herbivory, but by soil chemistry at the plot scale.
- In deserts with low winter precipitation and high temperatures and in deserts at higher elevations, phosphorus availability was most important in predicting annual grass cover.
- In deserts with higher winter precipitation and cooler temperatures, K availability was most important, with P and N availability being of secondary importance. Soil depth can also play a role in areas with very shallow soils.
- Because soil chemistry is mappable, resistance to invasion is also mappable. Factors operative at a local scale are applicable at a regional scale unless environmental conditions are very different. However, controls on annual grass appear different from region to region.

Do microhabitat characteristics or does soil chemistry determine field emergence and success of *Bromus tectorum*?

Introduction

The distribution and success of vascular plants is explained by both abiotic (e.g., water, light, nutrients) and biotic factors (e.g., neighboring plants and herbivores). Neighboring plants can alter the microenvironment experienced by a plant through increasing competition for resources. However, they can also facilitate plant growth by ameliorating otherwise harsh environmental conditions (Bertness and Callaway 1994, Callaway 1995). Plants can facilitate the growth of other plants by providing shade, litter, and protection from herbivores (Holmes and Jepson-Innes 1989, Hjältén et al. 1993, Hjältén and Price 1997). Shading from the canopy of other plants can have both positive and negative effects on plant species (Hastwell and Facelli 2003). Shade can negatively affect species by decreasing already low temperatures and decreasing the amount of available light, which is needed for photosynthesis. However, shade from plant canopies can provide refuge from high temperatures and decrease evapotranspiration rates (Chapin et al. 1994, Hastwell and Facelli 2003). Thus, facilitation via shade can be extremely important in harsh environmental conditions such as those found in desert ecosystems. The effect on a target plant of competition and facilitation from other plants may change throughout the different life stages of the target plant (Callaway et al. 1991, Facelli 1994, Callaway and Walker 1997).

Plant litter can affect plant germination, establishment, and distribution by altering the plant's microhabitat (Facelli and Pickett 1991, Wilby and Brown 2001, Dalling and Hubbell 2002, Liang and Seagle 2002). Litter can release nutrients to seedlings at initial growth stages and improve germination by maintaining moisture, providing nutrients and shade, and increasing the temperature surrounding the seed (Evans and Young 1970, Morris and Wood 1989, Facelli et al. 1999, Brearly et al. 2003). Although litter can increase germination through nutrient release, litter can also negatively affect germination if the litter contains allelopathic chemicals or if it prevents water from reaching the soil surface, thus prohibiting germination or reducing plant growth (Morris and Wood 1989, Chapin et al. 1994). Litter can also negatively affect plant growth by housing invertebrates that feed on seedlings (Facelli 1994).

Another factor shown to affect plant distributions are herbivores (Harper 1977, Louda et al. 1990). In general, herbivores have negative effects on plant performance (Harper 1977, Crawley 1983, Belsky 1986). However, some plant species have developed mechanisms to tolerate herbivory (McNaughton 1986, Paige and Whitham 1987, Trumble et al. 1993, Strauss and Agrawal 1999). Abiotic factors such as light, water and nutrients can also interact with herbivory to affect plant performance. Studies have shown that shade can increase or decrease damage by herbivores (Huffaker and Kennett 1959, Parker and Root 1981, Louda and Rodman 1983, Collinge and Louda 1988 a,b), and Maschinski and Whitham (1989) found nutrient availability determined the impacts of herbivores on *Ipomopsis arizonica*. In addition, litter and neighboring plants can influence herbivore damage by concealing seeds and small seedlings (McAuliffe 1984, Hjältén and Price 1997).

Soil nutrients have long been known to influence plant distribution and success. Studies efforts began as early as 1901 and continue to this day (e.g., Cowells 1901, Just 1947, Whittaker 1954, Wright and Mooney 1965,Wondzell et al. 1996, Lonsdale 1999).

Bromus tectorum is an exotic annual grass that has invaded millions of acres in the western United States and is the dominant plant species in many rangeland communities (Mack 1981). *B. tectorum* germinates in both fall and spring. However, the success of *B. tectorum*

appears to be higher in fall cohorts than in spring cohorts (Bookman 1983, Mack and Pyke 1983). In a *Pinus-Pseudotsuga* forest, litter had a negative effect on *B. tectorum* germination and the effects of the plant canopy varied between years (Pierson and Mack 1990). Evans and Young (1972) found that litter and rough soil surfaces increased soil moisture, favoring the establishment of *B. tectorum*. Herbivores have also been shown to have significant effects on *B. tectorum*. Pyke (1986) studied the effects of rodent herbivory on *B. tectorum* and found that herbivory had little effect on survival, but often removed large amounts of biomass. In addition, Pyke (1987) found rodent damage by herbivores was more detrimental to younger plants and survival decreased with increasing damage intensity.

In Canyonlands National Park, Belnap and Phillips (2001) documented that *B. tectorum* invaded areas dominated by *Hilaria jamesii* and only rarely in areas dominated by *Stipa hymenoides* and *S. comata*. At that time, Belnap and Phillips (2001) hypothesized that the *B. tectorum* invasion pattern could be explained by soil chemistry. However, microhabitat characteristics (the plant canopy, *H. jamesii* litter, herbivory by rodents) could also have explained this invasion pattern. Therefore, this experiment was designed to determine whether it was soil chemistry or microhabitat characteristics that enhanced *B. tectorum* invasion into the *Hilaria* community while conferring resistance to the *Stipa* community. We predicted the presence of a plant canopy and litter would increase *B. tectorum* emergence, survival and biomass, whereas herbivory would decrease *B. tectorum* success. We also predicted that *B. tectorum* would do best in soils from a *Hilaria*-dominated site.

Methods

Our field experiment was conducted near Squaw Flat Campground in the Needles District of Canyonlands National Park, Utah (1,525 m elevation). Soils at the sites are in the Begay series and are classified as fine sandy loam. Precipitation events and soil moisture at 10 cm were continuously logged using a Campbell data logger from September 1, 2001 until June 1, 2003. Two sites were located in areas dominated by the native perennial grass *H. jamesii*, (designated as North *Hilaria* and South *Hilaria* sites) and two sites were located in areas dominated by the native perennial grass *Stipa comata* (designated as North *Stipa* and South *Stipa* sites).

Microhabitat experiment

At each site we established 40 plots approximately 15 cm in diameter and manipulated the plant canopy, plant litter, and herbivory. All possible treatment combinations, along with controls, were used (8 treatments x 5 replicates x 4 sites = 160 plots). Plots were either placed in the canopy of *H. jamesii, S. comata*, or placed in the interspace, depending on the treatment. Hardware cloth cages (15 x 46cm, ¼" mesh) were placed over all plots. Half of the cages had access holes for rodents and the other half had no access holes. We placed 10 grams of *H. jamesii* litter, held down by a 1 cm nylon mesh, in the litter plots.

To determine whether the effects of the *H. jamesii* canopy were due to the presence of *H. jamesii* itself versus the effects of shade produced by *H. jamesii*, we also established 40 additional plots at the two *S. comata* sites. Plots were placed in the interspace where we could examine the effects of shade without the effects of competition. We mimicked shade by placing aluminum screen around the south side of the cages. *H. jamesii* litter was present in all plots (as it is present around all *H. jamesii* plants) and herbivory was manipulated by using cages with or without holes. These plots also controlled for any site differences there may have been between the *H. jamesii* and *S. comata* sites.

This experiment was conducted in the 2001-2002 and 2002-2003 growing season. We refer to these experiments as the 2001 and 2002 experiment respectively. Ten *B. tectorum* seeds were planted in each plot in September 2001. Total number of seedlings that emerged was recorded every month and the maximum number of seedlings that emerged was determined. After maximum emergence, seedlings were thinned to 5 well-established individuals. Due to subsequent drought conditions, survival was so low in May 2002 that biomass was unobtainable. The experiment was repeated by reseeding *B. tectorum* into the plots in September 2002. Aboveground tissue of plants from the 2002 planting was harvested and survival was recorded on May 29, 2003. Survival rate was determined as the number of individuals alive in the plot at the time of harvest. Biomass is reported as an average biomass per plant basis and was calculated by dividing the total pot biomass by the number of surviving individuals.

Emergence data were analyzed with a three-way ANOVA with the plant canopy, herbivory, and litter as fixed factors. Shade plots were analyzed separately in a two-way ANOVA with the plant canopy (canopy versus shade only) and herbivory as fixed factors. Biomass of *B. tectorum* individuals from 2002 was analyzed in the same manner. Total pot biomass was also analyzed, but is not presented because results showed similar patterns. Data were transformed when needed to meet ANOVA assumptions. Survival data from 2002 was analyzed using binary logistic regression. There were no site differences in any microhabitat analyses; therefore, all four sites were combined for analysis.

Reciprocal soil transplant experiment

We established 10 plots in all four sites (40 pots total). Entire soil cores were transplanted from the North *Hilaria* site to the North *Stipa* site, from the North *Stipa* site to the North *Hilaria* site, from the South *Hilaria* site to the South *Stipa* site, and from the South *Stipa* to the South *Hilaria* site. Soil cores were buried in PVC pipes approximately 15 cm in diameter and 30 cm in depth and care was taken so that there was minimal disturbance to the soil profile. All plots were placed in the plant interspace and hardware cloth cages (15 x 46 cm, ¼" mesh) were placed over all plots to prevent rodent herbivory. The reciprocal soil transplant experiment was conducted in the 2001-2002 and 2002-2003 growing season. In September 2001, ten *B. tectorum* seeds were planted, seedling emergence was monitored monthly, and after maximum emergence seedlings were thinned to 5 well-established individuals. Aboveground plant tissue was harvested in May 2002, dried at 60°C for 48 hours, and weighed. Ten new *B. tectorum* seeds were planted in September 2002, monitored, thinned and harvested in May 2003 as in the first growing season.

Emergence and biomass data were analyzed with a two-way ANOVA with site and soil as fixed factors. Biomass data is reported as an average biomass per individual per pot and was calculated by dividing the total pot biomass by the number of surviving individuals. Total pot biomass was also analyzed, but is not presented because results showed similar patterns. Data were transformed when needed to meet ANOVA assumptions. There were no site differences between North and South sites for either the *Hilaria* or *Stipa* sites; therefore, North and South *Hilaria* sites were combined and North and South *Stipa* sites were combined for analysis.

Subsets of the soil cores that were moved were analyzed for texture and chemistry. Phosphorus (Olsen et al. 1954) and available K (Schoenau & Karamonos 1993) were extracted with $NaHCO_3$. Zinc, Fe, Mn, and copper (Cu) were extracted with diethyltriaminepentaacetic acid (Lindsay & Norwell 1978). All exchangeable cations were extracted with ammonium acetate ($NH_4C_2H_3O_2$; Thomas 1982). Acid neutralizing potential (the combination of $CaCO_3$ and

oxides of Zn, Mn, Fe, and Mg) was measured by HCl neutralization (Allison & Moode 1965) and thus includes any soil constituents that neutralize acid. Texture was determined by the hydrometer method and total N was determined by Kjeldahl analysis (Bremner 1996). Cation exchange capacity was analyzed by sodium saturation followed by ammonium displacement (Rhoades 1982).

Results

Precipitation and soil chemistry

Soil chemistry for *S. comata* and *H. jamesii* sites is reported in Table 1. Average annual precipitation for the Needles District of Canyonlands National Park is 216 mm; however, the total precipitation during our 2001-2002 experiment (8 months) was only 55 mm. During the three months that lapsed between experiments, Needles received 34 mm of precipitation. Total precipitation was 169 mm in the 2002-2003 growing season (9 months) and was thus three times greater than that received during the 2001-2002 growing season. Soil moisture at 10 cm was very different in 2001 than it was in 2002 (Figure 1). In 2001, high moisture was sustained throughout the spring growing season for *Bromus*. In 2002, however, soil moisture declined abruptly throughout the growing season.

	Stipa	*Hilaria*
P (ppm)	5	9
Total N (ppm)	173	179
Available K (ppm)	91	162
Zn (ppm)	0.3	0.3
Fe (ppm)	2.0	2.2
Mn (ppm)	3.2	3.6
Cu (ppm)	0.4	0.5
Exchangeable Ca (ppm)	3146	3179
Exchangeable Mg (ppm)	122	148
Exchangeable K (ppm)	172	266
Exchangeable Na (ppm)	57	58
Acid neutralizing potential (%)	6	5
Sand (%)	73	73
Clay (%)	12	13
Silt (%)	15	15
Cation exchange capacity (EC meq\100g)	5	5

Table 1 Soil chemistry of *Stipa comata* and *Hilaria jamesii* dominated sites in Squaw Flat, Needles District, Canyonlands National Park.

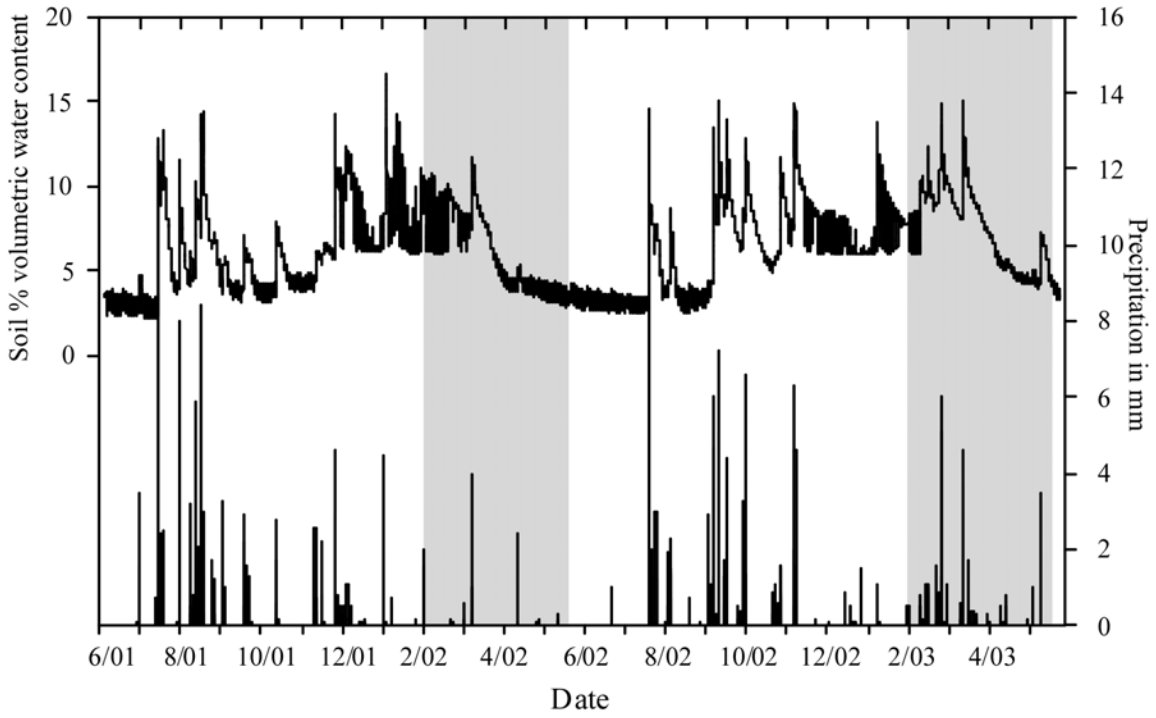

Figure 1 Rain events at Squaw Flat from September 25, 2001 to May 29, 2003, which covered the span of the 2001-2002 and 2002-2003 experiments.

Microhabitat experiment

Emergence

When all treatments were combined, emergence was 2.69 ± 0.16 seedlings per plot in 2001 and 9.07 ± 0.11 seedlings per plot in 2002. In 2001, the plant canopy had a positive effect on *B. tectorum* emergence (Figure 2, $P_{canopy} < 0.0001$), being 65% higher under the plant canopy than in the interspace. Herbivory had a negative effect on *B. tectorum*, reducing emergence by 27% ($P_{herbivory} < 0.0001$). *H. jamesii* litter increased *B. tectorum* emergence by 19% ($P_{litter} = 0.05$). In addition, litter affected emergence differently under the plant canopy versus in the interspace ($P_{litter\ x\ canopy} = 0.023$). In the interspace, litter decreased *B. tectorum* emergence by 8% whereas litter increased emergence under the plant canopy by 27%. There was no significant interaction between litter and herbivory ($P_{litter\ x\ herbivory} = 0.933$) or the plant canopy and herbivory ($P_{canopy\ x\ herbivory} = 0.169$). In a pair-wise comparison, emergence of *B. tectorum* under the plant canopy with herbivory (simulating the natural situation) was higher when litter was present than when litter was absent ($P = 0.004$).

Artificial shade had no effect on *B. tectorum* emergence ($P_{shade} = 0.117$), nor did herbivory under artificial shade conditions ($P_{herbivory} = 0.247$). There was also no interaction between herbivory and shade ($P_{herbivory\ x\ shade} = 0.247$). In a pair-wise comparison, when herbivory was excluded, shade tended to have a positive effect on *B. tectorum* emergence ($P = 0.057$).

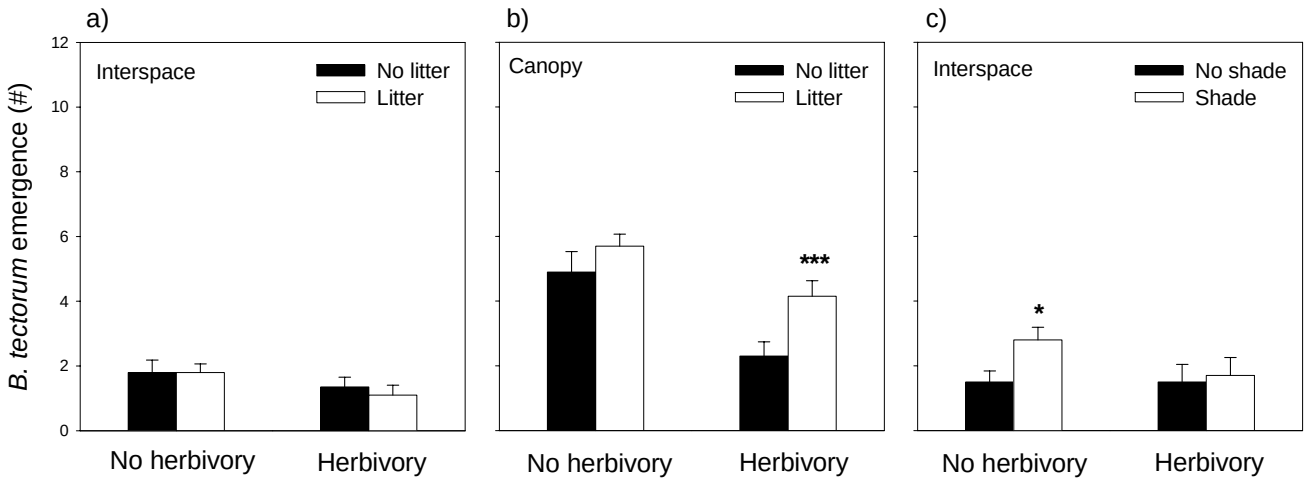

Figure 2 Effects of herbivory on emergence of *Bromus tectorum* seedlings (out of 10) in 2001 when a) in the interspace with and without litter, b) under the canopy with and without litter, and c) in the interspace with litter when artificial shade is present or not present. Error bars represent ± 1 standard error. * = $P \leq 0.10$; ** = $P \leq 0.05$; *** = $P \leq 0.001$.

In contrast to the drought year (2001), the almost average year (2002) showed no effects of the plant canopy, herbivory or litter on *B. tectorum* emergence (Figure 3). In 2002, *B. tectorum* emergence was similar under the plant canopy and in the interspace ($P_{canopy} = 0.642$). Herbivory tended to decrease *B. tectorum* emergence ($P_{herbivory} = 0.089$) and the addition of litter did not affect emergence ($P_{litter} = 0.327$). There were no significant interactions among the canopy, litter, or herbivory ($P_{canopy\ x\ herbivory} = 0.642$; $P_{litter\ x\ canopy} = 0.380$; $P_{litter\ x\ herbivory} = 0.959$).

Examining the role of shade in 2002 revealed similar patterns to 2001. In the interspace, shade had no effect on *B. tectorum* emergence ($P_{shade} = 1.000$). Herbivory also did not affect *B. tectorum* emergence ($P_{herbivory} = 0.415$) and did not interact with shade to affect emergence ($P_{herbivory\ x\ shade} = 0.540$).

Biomass

Biomass data was only obtainable from plants that survived in the 2002 experiment. Similar to emergence in 2002, the plant canopy, herbivory and *H. jamesii* litter had no significant effects on the final shoot biomass of *B. tectorum* (Figure 4). *Bromus tectorum* biomass was not affected by being under the plant canopy ($P_{canopy} = 0.141$) and herbivory did not decrease *B. tectorum* biomass ($P_{herbivory} = 0.799$). Also, adding litter did not affect the biomass of *B. tectorum* ($P_{litter} = 0.724$). No interactions occurred between the canopy, herbivory, and litter ($P_{canopy\ x\ herbivory} = 0.679$; $P_{litter\ x\ canopy} = 0.793$; $P_{litter\ x\ herbivory} = 0.884$). When examining the effects of shade, biomass was similar with and without shade ($P_{shade} = 1.000$), with and without herbivory ($P_{herbivory} = 0.293$), and herbivory did not interact with shade to affect biomass ($P_{herbivory\ x\ shade} = 0.285$).

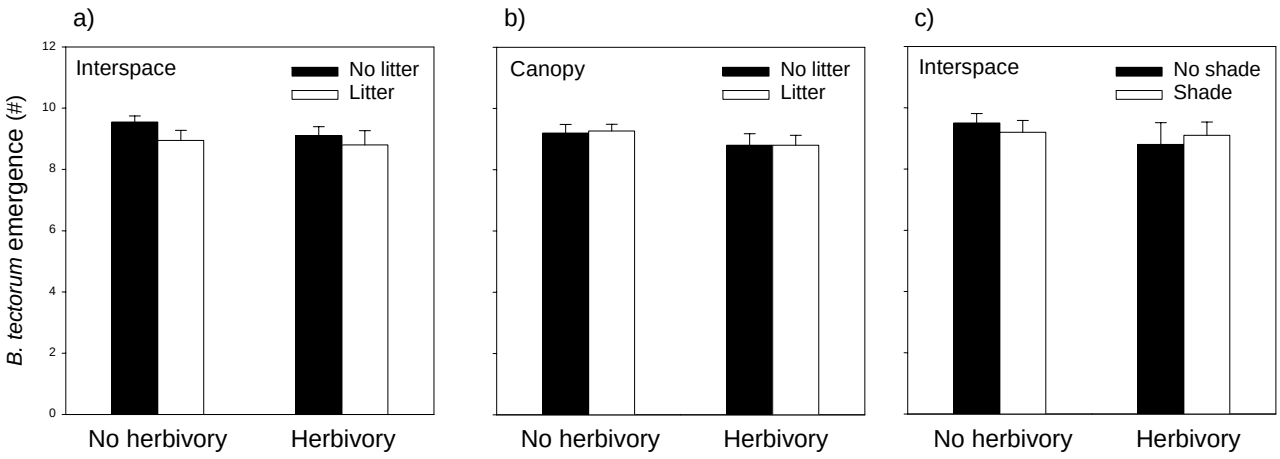

Figure 3 Effects of herbivory on emergence of *Bromus tectorum* seedlings (out of 10) in 2002 when a) in the interspace with and without litter, b) under the canopy with and without litter, and c) in the interspace with litter when artificial shade is present or not present. Error bars represent ± 1 standard error.

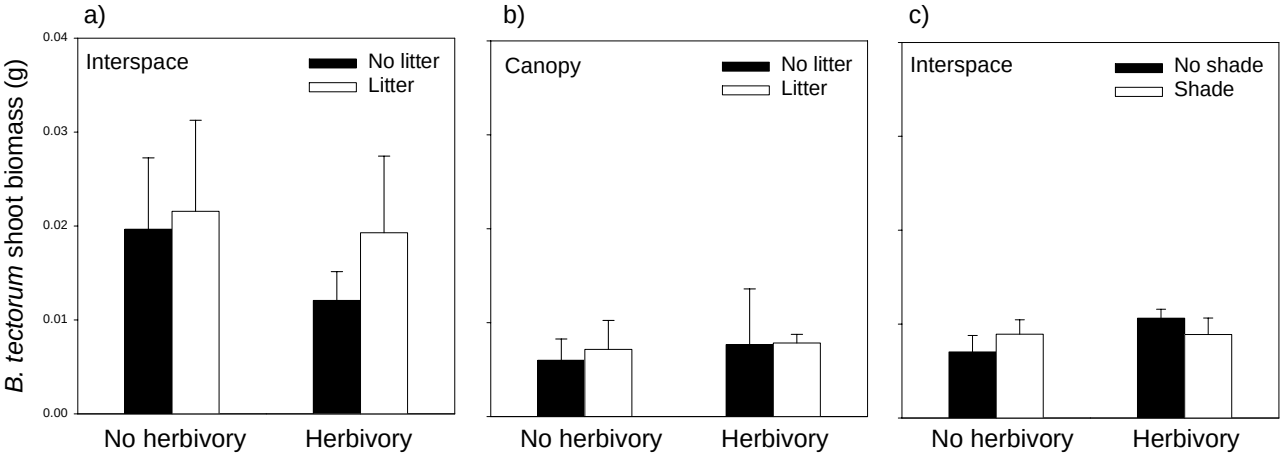

Figure 4 Effects of herbivory on *Bromus tectorum* shoot biomass in 2002 when a) in the interspace with and without litter, b) under the canopy with and without litter, and c) in the interspace with litter when artificial shade is present or not present. Error bars represent ± 1 standard error.

Reciprocal soil transplant

In 2001 there was no difference between *H. jamesii* and *S. comata* sites on *B. tectorum* emergence or biomass; therefore, sites were combined for analysis. When sites were combined, *B. tectorum* emergence was higher in *H. jamesii* soils than in *S. comata* soils (Figure 5, df = 1, F = 4.861, P_{soil} = 0.03), but the biomass of *B. tectorum* did not differ when planted either soil (df = 1, F = 0.135, P_{soil} = 0.71). In 2002, *H. jamesii* and *S. comata* sites affected *B. tectorum* emergence similarly; therefore, in the combined analysis *B. tectorum* emergence tended to be higher in *H. jamesii* soils than in *S. comata* soils (df = 1, F = 3.585, P_{soil} = 0.07). Whereas there were significant differences in *B. tectorum* biomass in 2002 that depended upon the interaction between site and soil type (ANOVA: df = 1, F = 0.825, P_{site} = 0.37; df = 1, F = 0.411, P_{soil} = 0.53, df = 1, F = 0.4.187, $P_{site\ x\ soil}$ = 0.05), the overall biomass was so small that these results are probably not biologically significant.

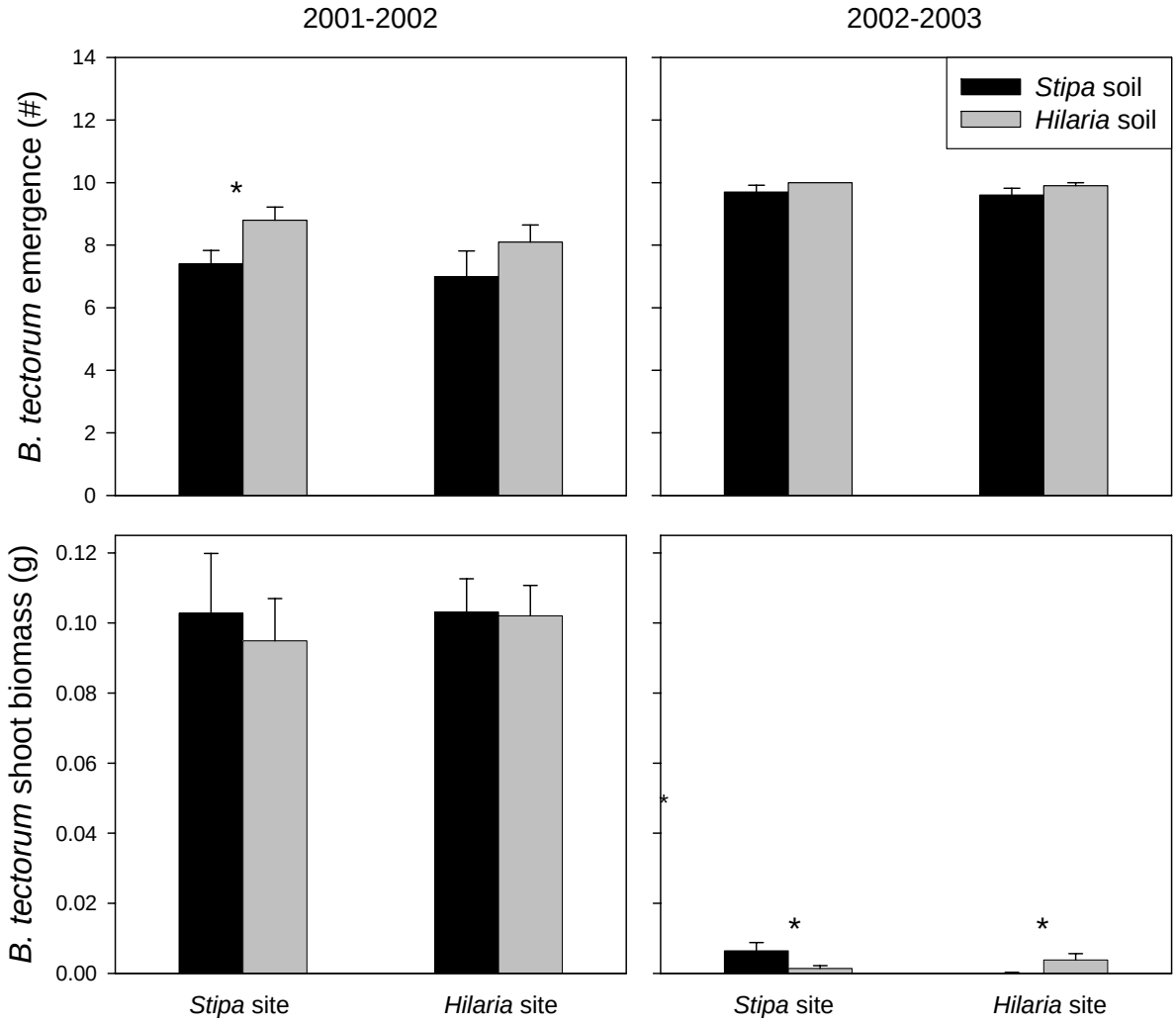

Figure 5 Emergence and biomass of *Bromus tectorum* in 2001-2002 and 2002-2003 when planted in soil from a site dominated by either *Hilaria jamesii* or *Stipa comata*. Soil remained in its original site or was transplanted to a site of the opposite plant species.

Discussion

Our results suggest that *B. tectorum* emergence and survival are negatively affected by extremely low precipitation and a lack of fall rains prior to October, as occurred in 2001. Although precipitation in 2002 was still lower than average, overall emergence was three times greater in 2002 than 2001. In addition, the extreme drought in 2001 had negative effects on survival, as survival in 2002 was 22 times greater than in 2001. This is not surprising since precipitation in 2002 was approximately three times greater than in 2001. Evans et al. (1970) studied *B. tectorum* growth and phenology over 3 years and found it to widely vary depending on the amount and timing of precipitation. Low precipitation years may negatively affect *B. tectorum*;

however, high seed production creates large pre-existing seed banks that likely maintain infestations of *B. tectorum*.

Being under the canopy of a plant increased the emergence of *B. tectorum* under drought conditions, but did not affect emergence in the almost average year. Young and Evans (1975) also found recruitment of *B. tectorum* was higher under shrub canopies in the sagebrush steppe. Being under the canopy could benefit *B. tectorum* by decreasing extreme light that could cause photoinhibition; increasing access to soil moisture, plant litter, and/or soil nutrients; or providing protection from herbivores. However, our results suggest these mechanisms do not explain the positive effects of being under the canopy. Shade, which would mimic the effects of a plant canopy by decreasing light and increasing soil moisture, did not positively affect *B. tectorum*. In addition, litter did not increase the success of *B. tectorum*. The effects of soil nutrients near neighboring plants was not examined in this study; however, we suspect that *B. tectorum* benefits from soil nutrient patches surrounding neighboring plants or *B. tectorum* obtains nutrients from neighboring plants, perhaps by tapping into their mycorrhizal fungi (Belnap et al. in review).

In contrast to the positive effects of the plant canopy on *B. tectorum* emergence, being under a plant canopy had no effect on biomass and significantly decreased survival in this study. Pierson and Mack (1990) also found the effects of plant canopies to change over the life cycle of *B. tectorum*, although their results differed from results of this study. In a *Pinus-Pseudotsuga* forest, plant canopies had no effect on recruitment and increased survival in one year, while increasing recruitment and not affecting survival in another year. It is difficult to compare these studies due to differences in ecosystems. Nevertheless, these studies suggest that the effects of the plant canopy may change over time and it may be difficult to predict the effects of plant canopies on *B. tectorum*. Additional water and nutrients under the plant canopy may have stimulated germination of the *B. tectorum* seed, but the seedling soon finds itself out-competed by the adjacent adult plant.

As found for the effects of the plant canopy, the effects of herbivory differed between the drought and almost-average year. Herbivores had a negative effect on emergence in the drought year, but not in the almost-average year. *Bromus tectorum* likely provides an extra food source for rodents in the fall and winter when some rodents switch from an insect and seed diet to eating foliage in the winter (Pyke 1986). The higher impact of herbivores on seedling emergence in the drought year may have been due to extremely low availability of native plants as a food source.

The biomass of *B. tectorum* seedlings that survived emergence was not affected by herbivory. This suggests that predation may only be important when *B. tectorum* seedlings emerge but not once seedlings are established. It is also possible that *B. tectorum* compensated for tissue lost to herbivory. Other studies have demonstrated tolerance of plants to herbivores, which may be affected by plant competition, nutrient availability, and timing of damage (Maschinski and Whitham 1989, Whitham et al. 1991, Strauss and Agrawal 1999). Pyke (1987) found that grazing at early life stages of *B. tectorum* decreased seedling density, but those individuals who survived produced more seeds, suggesting compensatory growth in reproduction or reduced intraspecific competition. If our observed lack of herbivore effects was due to compensatory growth in biomass by *B. tectorum*, it appears that the compensation was not affected by plant competition since the effects of herbivory on biomass were similar under the canopy of a competitor and in the interspace. Compensatory growth may be reduced in drier years; however, low survival in the drought year made it impossible to determine the effects of herbivory on biomass.

Herbivory did not affect the biomass of *B. tectorum*, but did decrease *B. tectorum* survival in this study. This contrasts with the results of Pyke (1986) where he found rodent grazing to have negative effects on biomass and no effect on survival. In our experiment, the negative effects on survival, but not on biomass, suggest that herbivores ate the entire plant rather than consuming small amounts of the plant. Although we did not assess percent damage in this study, Pyke (1986) observed that herbivores usually removed the entire aboveground biomass. Pyke attributes the survival of *B. tectorum* survival after herbivory to a well-developed root system, thus stabilizing plants when they are attacked by rodents. Soils at our study site may be sandy enough that animals pull *B. tectorum* out by the roots when the plant is tugged on. In addition, survival may have decreased if plants were eaten when very small and had insufficient root biomass to allow for shoot regrowth.

As predicted, *H. jamesii* litter increased *B. tectorum* emergence and these positive effects were increased in plants under the canopy; however, these positive effects only occurred during the drought year. The plant canopy likely worked in concert with litter to increase soil moisture, which was probably extremely low under drought conditions. However, *B. tectorum* did not appear to need this increased moisture in the almost-average year. Similar variations in the effects of litter on *B. tectorum* emergence have been found in other studies. A study conducted in a *Pinus-Pseudostuga* forest found litter to have no effect on *B. tectorum* recruitment unless litter levels were thick (Pierson and Mack 1990). Unfortunately, their study did not examine the interactions between plant litter and the plant canopy. Another study in a big sagebrush community found litter to increase germination and establishment of *B. tectorum* (Evans and Young 1997). Abiotic and biotic differences in plant communities may explain the varying effects of litter on germination and emergence.

We also found the effects of *H. jamesii* litter changed over the life cycle of *B. tectorum* as shown for the effects of the plant canopy and herbivory. Although litter increased *B. tectorum* emergence, litter had no effect on the biomass of *B. tectorum* and actually decreased its survival. Litter may increase emergence by increasing soil moisture; however, previous studies have shown that litter can also have negative effects on plants due to allelopathic chemicals leached from plant material (Morris and Wood 1989, Chapin et al. 1994). The release of allelopathic chemicals may not have been immediate in our experiment; therefore, the negative effects of litter did not affect *B. tectorum* emergence and biomass, but negatively affected survival. Litter may have also decreased survival by preventing the small rain events that occurred during our experiment from reaching seedling roots. Litter may also have harbored microinvertebrates that feed on *B. tectorum* or pathogens (Facelli et al. 1999, Garcia-Guzman and Benitez-Malvido 2003).

Belnap and Phillips (2001) hypothesized that *B. tectorum* occurred more frequently in areas dominated by *H. jamesii* than *S. comata* due to differences in soil chemistry in these areas. Our reciprocal soil transplant experiment confirms this hypothesis and suggests the higher occurrence of *B. tectorum* in *H. jamesii* dominated areas is due to soil chemistry at *H. jamesii* sites rather than the microhabitat created by *H. jamesii*. However, the differences seen in B. tectorum and biomass were not very large. Therefore, although this appears to be the most likely explanation, this experiment should be repeated in years of above-average moisture, which is when *B. tectorum* invasions occur in this region.

Summary

Our results suggest that several abiotic and biotic factors affect *B. tectorum*, which vary between years and throughout the life cycle of *B. tectorum*. We found that both timing and amount of precipitation strongly influence the emergence, biomass and survival of *B. tectorum*. Effects of the plant canopy, *H. jamesii* litter and herbivory were variable, depending on precipitation. In the drought year, there were facilitative effects of the canopy and litter on seedling emergence. In the almost-average year, the plant canopy and litter had no effect on emergence and biomass, but eventually decreased survival. The effects of herbivory also changed in the almost-average year where herbivory only had negative effects on the survival of *B. tectorum*. Our results support other studies that show facilitative and competitive interactions may change throughout a plant's life cycle and depend on abiotic conditions.

We hypothesized that the reason *B. tectorum* is found more frequently in soils dominated by *H. jamesii* than soils dominated by *S. hymenoides/S. comata* was due to the microhabitat created by *H. jamesii*. Although we found several microhabitat factors to influence *B. tectorum,* these factors did not differ between patches of *H. jamesii* and *S. comata*. This suggests that although these factors influenced *B. tectorum* success, they did not explain the observed association between *B. tectorum* and *H. jjamesii*. We found, instead, that the patterns of *B. tectorum* invasion into *H. jamesii* areas are likely better explained by soil chemistry, although this relationship was weak.

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Predicting current and future distributions of exotic annual grasses

(Will be submitted to Conservation Biology)

Introduction

Scientists have long been attempting to document variables that control the distribution of plants and plant communities (e.g., Cowells 1901, Just 1947, Whittaker 1954, Wright and Mooney 1965, Wondzell et al. 1996, Lonsdale 1999). Special interest has been paid to variables that appear to confer resistance to invasion on native communities. Efforts have focused on both individual species characteristics (e.g., Heger and Trepl 2003), other biotic factors such as the presence or diversity of plant and/or soil species or functional groups (e.g., Callaway et al. 2004; Foster et al. 2002; Levine 2000; Levine and D'Antonio 1999; Stohlgren 2002; Stohlgren et al. 1999, 2003; Tilman 1997) and abiotic factors such as climate and soils (e.g., Billings 1950; Hoopes and Hall 2003; Stohlgren et al. 1999, 2001; Foster et al. 2002).

Non-native annual grasses from the Mediterranean and Asian steppe regions (*e.g., Bromus tectorum, B. madretensis, Schismus arabicus*) have spread rapidly across the drylands of the western United States. These grasses now dominate hundreds of millions of hectares acres the West, with many more lands at high risk from invasion (Whisenant 1990). Where these annual grasses dominate, native plant and animal diversity is reduced and species sometimes extirpated (Rosentreter 1994), fire frequencies are often increased (Whisenant 1994), community productivity is decreased, and soil biota and nutrient cycles are altered (Belnap and Phillips 2001, Evans et al. 2001). Despite much research, what makes an ecosystem susceptible to invasion to annual grasses is still not known and very little is known about what determines different recovery trajectories (Pyke and Novak 1994; Sparks et al. 1990).

Unfortunately, almost all efforts to contain or eliminate *Bromus* have been unsuccessful (Evans and Young 1984; Monsen 1994). Therefore, attention has now turned to ways to prevent *Bromus* invasion. To do this, we need an understanding of which factors promote, and which prevent, invasion. Soil surface disturbance is the factor most often ascribed responsibility for annual grass invasion (Baker 1986, Hobbs 1989, Rejmánek 1989, Hobbs and Huenneke 1992, Bergelson et al. 1993, Burke and Grime 1996). The fact that annual grasses are usually associated with environments physically disturbed by livestock grazing or other soil surface-disturbing activities (Klemmedson and Smith 1964, Upadhyaya et al. 1986) suggests that disturbance enhances invasion. However, annual grasses have also established and persisted in relatively undisturbed bunchgrass communities (Daubenmire 1947, Hulbert 1955, Tausch et al. 1994), indicating there are other factors influencing the invasibility of ecosystems. A recent *Bromus tectorum* invasion occurred in Canyonlands National Park in a remote, never-grazed grassland with very little human visitation (Belnap and Phillips 2001). This invasion occurred in small and distinct patches, indicating that at least in this locality, invasion was controlled by local environmental characteristics such as vegetative cover, ground cover or soils.

The patchy nature of this invasion spurred us to examine whether annual grass invasions were also patchy in other semi-arid and arid regions, and if so, what was different about the invaded patches and whether these factors were applicable at a landscape and/or regional scale. By understanding characteristics of areas invaded by annual grasses relative to adjacent uninvaded areas, we also hoped to gain insight into what factors might promote invasion as well as factors that might be used to retard or prevent invasions. We focused our efforts on sites in

both hot deserts (Chihuahuan, Mojave) and cool deserts (Colorado Plateau, Great Basin) in the SW United States.

Methods

Study site selection: Study sites were located in areas with either surficial geology maps or completed soil surveys. Sample locations within these areas were to represent each of the soil or surficial units. Wherever possible, sites were chosen that contained adjacent patches of annual grass-invaded and uninvaded soils. The 38 sites in the Chihuahuan desert centered around Las Cruces NM (Figures 1 and 2). The 172 sites in the Mojave Desert were scattered throughout the desert, although most were in the north and east Mojave (Figures 1 and 3). The 184 Colorado Plateau sites were located in SE Utah (Figures 1 and 4). The 38 Great Basin sites were located north of the Great Salt Lake and in southern Idaho (Figures 1 and 5).

Sample collection and analyses: Site characteristics were recorded at each location, including elevation, latitude and longitude, slope, aspect, landscape position, and parent material. Ground cover (lichens, mosses, rocks in three size classes, ground litter, bioturbation) and cover of plants by functional group (forbs, perennial grasses, exotic annual grasses, shrubs) was estimated every 1 m along three 100m line transects. Along these lines, soil samples were collected at two depths (0-0.5 and 0-10 cm) at each stop and composited for analysis. Both depths were sent to the Brigham Young University soil lab for analysis. Phosphorus (P; Olsen et al. 1954) and available potassium (K; Schoenau & Karamonos 1993) were extracted with $NaHCO_3$. Zinc (Zn), iron (Fe), manganese (Mn), and copper (Cu) were extracted with diethyltriaminepentaacetic acid (Lindsay & Norwell 1978). All exchangeable cations (calcium [Ca], magnesium [Mg], sodium [Na], and K) were extracted with ammonium acetate ($NH_4C_2H_3O_2$; Thomas 1982). Acid neutralizing potential (the combination of calcium carbonate [$CaCO_3$] and oxides of Zn, Mn, Fe, and Mg) was measured by HCl neutralization (Allison & Moodie 1965) and thus includes any soil constituents that neutralize acid. Texture was determined by the hydrometer method and total N was determined by Kjeldahl analysis (Bremner 1996). Soil pH was determined electrometrically with a saturated soil paste made with distilled water. Soil cation exchange capacity (CEC) was determined by saturating the soil exchange complex with Na acetate, displacing exchangeable Na with NH4 acetate, and measuring displaced Na by atomic absorption. The 0-0.5 soils were analyzed for chlorophyll *a* to estimate cyanobacterial biomass.

Statistical analyses: Statistics were run using SPSS v.12 and S-Plus. For all analyses except the regression trees, data were first tested for normality using a Kolmogorov-Smirnov statistic, with a Lilliefors significance level for testing normality. Levene's test was used to examine the equality of variances, and both pooled and separate variance t-tests were used to examine for equality of means. Non-normal data was transformed, or if that was not possible, equivalent non-parametric tests were used.

Because we found no annual grasses at the Chihuahuan site, only the soil chemistry data was analyzed from that site. Stepwise linear regression was used to predict annual grass cover at the Mojave, Great Basin, and Colorado Plateau sites before and after the sites were divided into elevation classes. All Great Basin sites were collected as paired invaded and uninvaded sites, and thus we also employed both regression analyses and a paired t-test to analyze those sites.

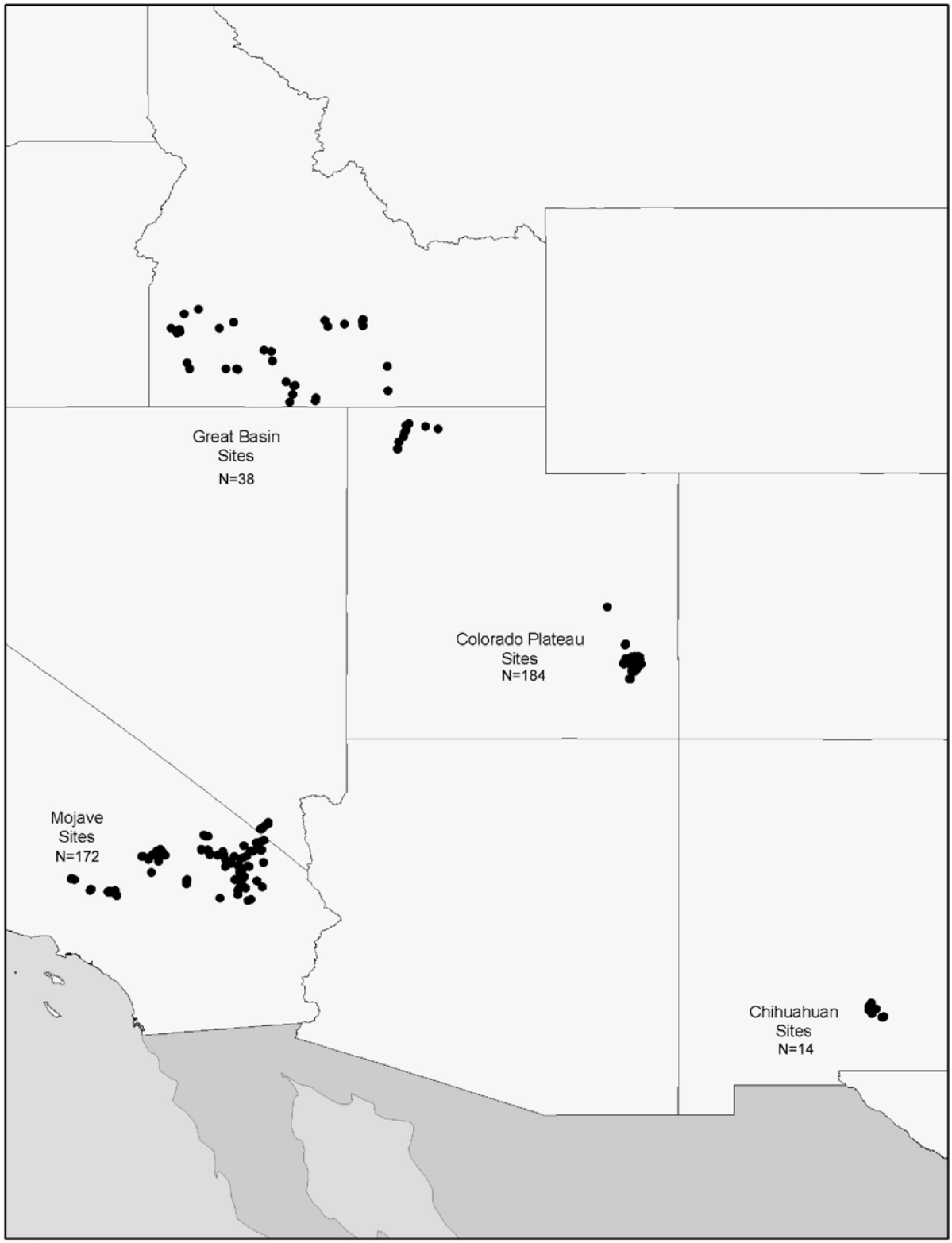

Figure 1. Location of study sites in the Chihuahuan, Mojave, Colorado Plateau, and Great Basin deserts.

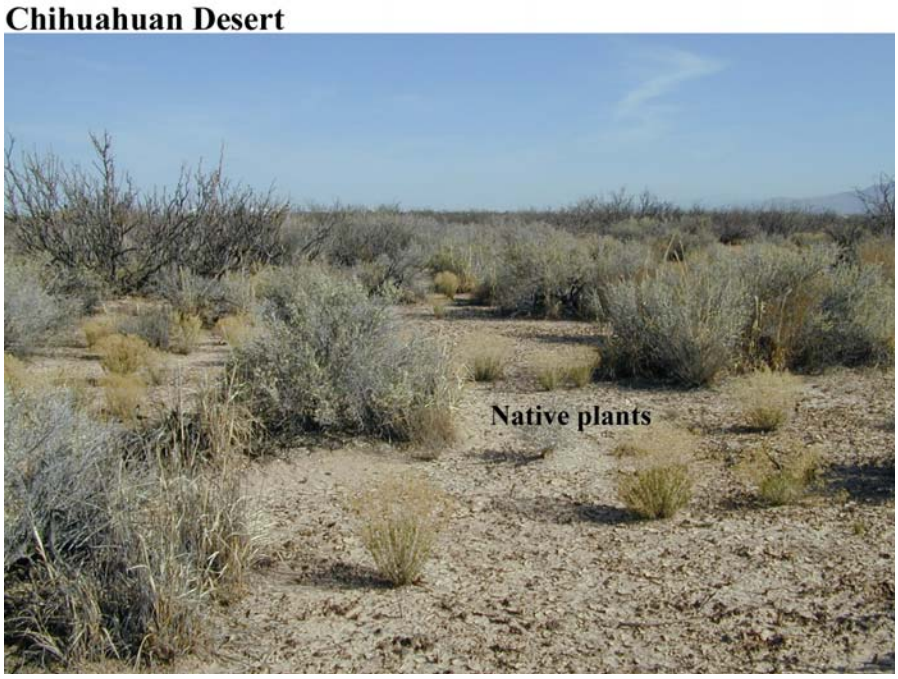

Figure 2. Photo of *Bromus* and native plant patches in the Chihuahaun desert.

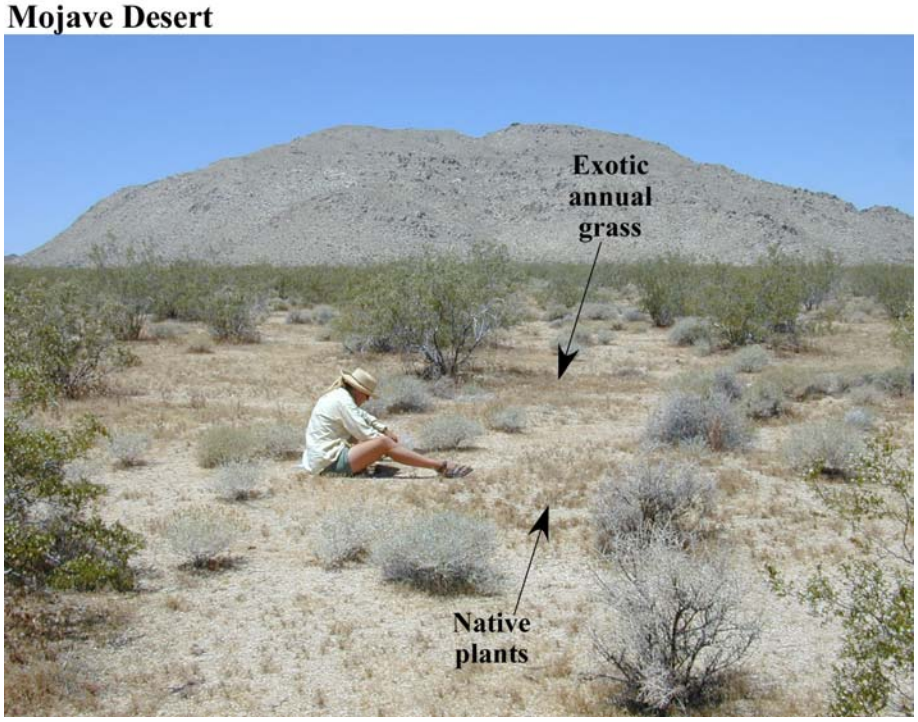

Figure 3. Photo of *Bromus* and native plant patches in the Mojave desert.

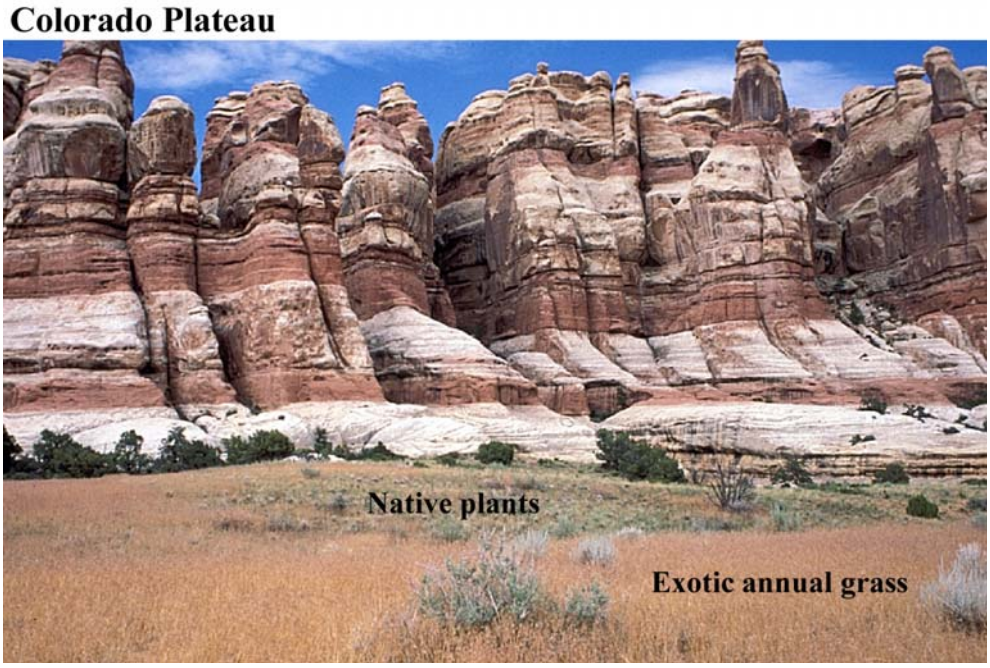

Figure 4. Photo of *Bromus* and native plant patches in the Colorado Platueau

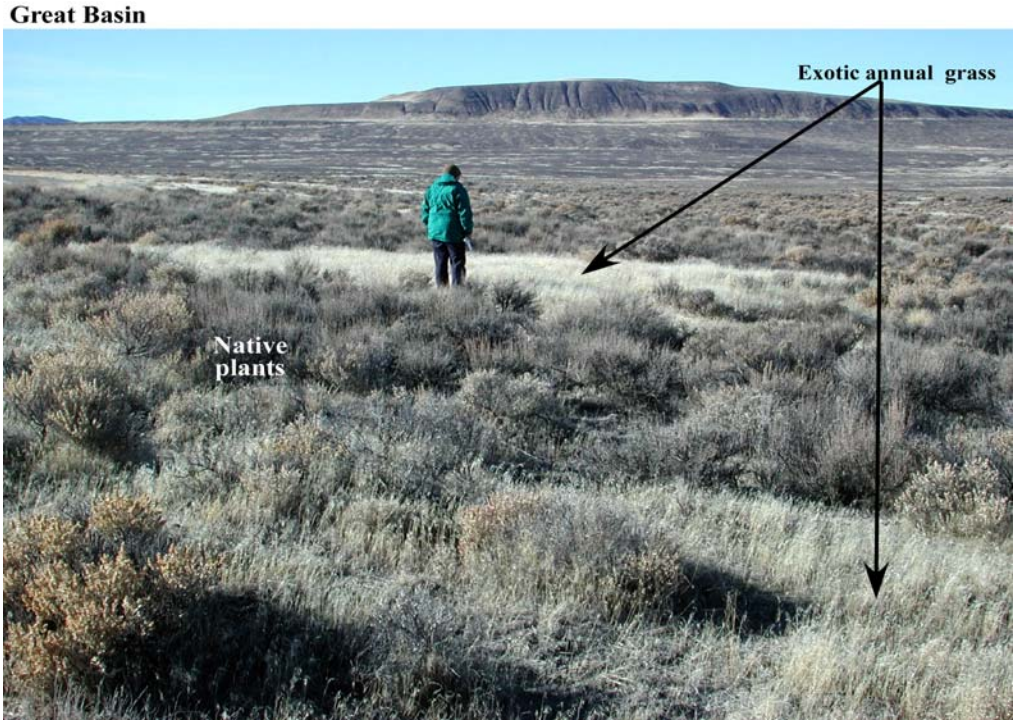

Figure 5. Photo of *Bromus* and native plant

Regression tree analyses (Iverson and Prasad 1998, Franklin 1998, De'Ath and Fabricius 2000) was also used to determine response thresholds for the different variables. This type of analysis is much more flexible in uncovering structure in data that have variables that may be hierarchical, non-linear, non-additive, or categorical in nature (Iverson and Prasad 1998). For regression trees in the Great Basin, we used percent cover classes for the predictive variable.

We sampled the Colorado Plateau more intensely than the other regions, using three scales of sampling. We first intensively sampled a small area (80 ha), then an intermediate area that contained the smaller area (8,100 ha) and then the entire watershed (70,000 ha). For the small and intermediate area analysis, data was collected paired invaded and uninvaded pairs and paired t-tests were used for the analysis of this data. At the watershed scale, sites were independent and thus stepwise regression and regression trees were used for analysis. For the regression tree analysis, we classified *Bromus* in three ways: cover classes, absolute cover, and presence/absence (>10% indicated presence). Because results were similar among these three approaches and our intent was to produce a model easily used and understood by land managers, we chose to work with the presence/absence model. We also asked three different questions with the regression tree analysis, and thus used three different data sets: 1) From a researcher's perspective, what factors were best correlated with annual grasses? For this analysis, we used all available data; 2) From a manager's perspective, what factors best predicted annual grass cover, using only data obtainable from a soil survey, a geology map, and a topographic map (i.e., parent material, cations, pH, CEC, soil texture, elevation, slope, aspect, heat load); and 3) From a manager's perspective, what factors best predicted annual grass cover using only data from a soil survey and a topographic map? For this analysis, we only used cations, CEC, pH, and soil texture.

	Mojave		Great Basin		Co Plateau		Holloman	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
P	0.8	26.6	10.9	60.2	0.9	37.3	0.1	25.6
K available	40	530	125	1130	38	816	10	1005
pH	6.4	8.0	4.9	8.1	7.0	9.0	6.5	8.0
Sand	42	95	13	77	22	93	33	70
Clay	4	28	12	40	4	51	14	34
Silt	1.0	40.2	11.0	59.0	0.4	52.0	21.1	40.3
CEC	1	32			1	61	1	22
Zn	0.12	0.81	0.45	8.25	0.06	3.53	0.02	1.61
Fe	0.9	14.3	3.8	83.6	1.0	63.2	0.4	3.1
Mn	0.7	14.4	6.0	113.2	0.4	32.4	0.3	10.4
Cu	0.12	1.69	0.88	3.68	0.05	5.22	0.01	1.54
Ca exchangeable	500	5796	961	4842	1012	26880	2384	54620
Mg exchangeable	29	693	121	849	31	820	10	7272
K exchangeable	29.72	1053.21	270.64	1724.40	25.62	887.60	0.01	1554.60
Na exchangeable	0.1	1012.5	51.6	979.6	0.2	912.4	25.5	30180.0
Total N	1	1463	369	2551	39	6994	33	1427
$CaCO_3$	0.05	26.53	0.03	28.24	0	63.00	0.34	35.01
K/Mg	0.64	6.2	0.46	4.29	0.13	4.6	0.04	5.2
$P/CaCO_3$	0.13	166.00	0.55	528.00	0.04	391.00	0.06	1.50
Perennial plant % cover	0	57	12	80	0	80	14	50

Table 1. The range of nutrients, nutrient ratios and perennial plant cover in the different deserts sampled. Note that although no annual grass patches were found at any of our study sites in the Chihuahuan desert, soil chemistry, soil texture, and plant cover were within the range found in the other deserts, where annual grasses were abundant.

Mojave			
	Predictor	**R^2**	**Correlation sign**
All sites	$P/CaCO_3$	0.36	+
All sites with >4% annual grass	$P/CaCO_3$	0.93	+
200-500 m	Ca exchangeable	0.26	-
	Mn	0.46	+
	Zn	0.64	-
	Na exchangeable	0.73	-
500-950 m	$P/CaCO_3$	0.47	+
	K/Mg	0.55	+
	Cu	0.62	-
950-1100 m	Mn	0.08	+
>1100 m	$P/CaCO_3$	0.25	+
	Silt	0.46	+
	Ave. annual ET	0.70	+
	Ca exchangeable	0.78	-
	Clay	0.85	-
	Elevation	0.91	-

Table 2. Results of a stepwise regression model for sites in the Mojave desert for all sites combined. Because we believed soil chemistry would vary with available precipitation and thus elevation, we also divided the sites into four categories based on elevation: 200-500 m, 500-950m, 950-1100 m, and >1100m. No stepwise regression model satisfactorily predicted annual grass cover from 950-1100m elevation.

Results

Chihuahuan Desert: No annual grass patches were found at any of our study sites or on any soil type. This was despite vegetation cover and soil nutrients at these sites being well within the range found in the other deserts (Table 1).

Mojave Desert: When all data were entered into the stepwise regression model, the only predictor of annual grass cover was positive relationship with $P/CaCO_3$ ($R^2 = 0.36$). When we restricted the inquiry to sites with >4% annual grass cover, $P/CaCO_3$ had an R^2 of 0.83. Because we believed that the factors affecting annual grass distribution would vary with available precipitation, we then divided the sites into four categories based on elevation: 200-500 m, 500-950 m, 950-1100 m, and >1100m (Table 2). For the lowest elevation sites, the soil nutrients Ca, Zn, and Na were negatively correlated, and Mn positively correlated, with annual grass cover

		Bromus dominated		*Stipa-Sporobolus* dominated		
Variables	**n**	**Mean**	**Std. error**	**Mean**	**Std. error**	**p value**
K, ppm	13	346	±50	145	±13	0.0001
K/Mg	13	1.4	±0.16	0.76	±0.1	0.0001
K/Ca	13	0.05	±0.01	0.02	±0	0.0001
CEC	6	0.66	±0.03	0.52	±0.02	0.0003

Table 3. A comparison of paired Colorado Plateau sites with and without annual grasses at the intermediate scale (8000 ha).

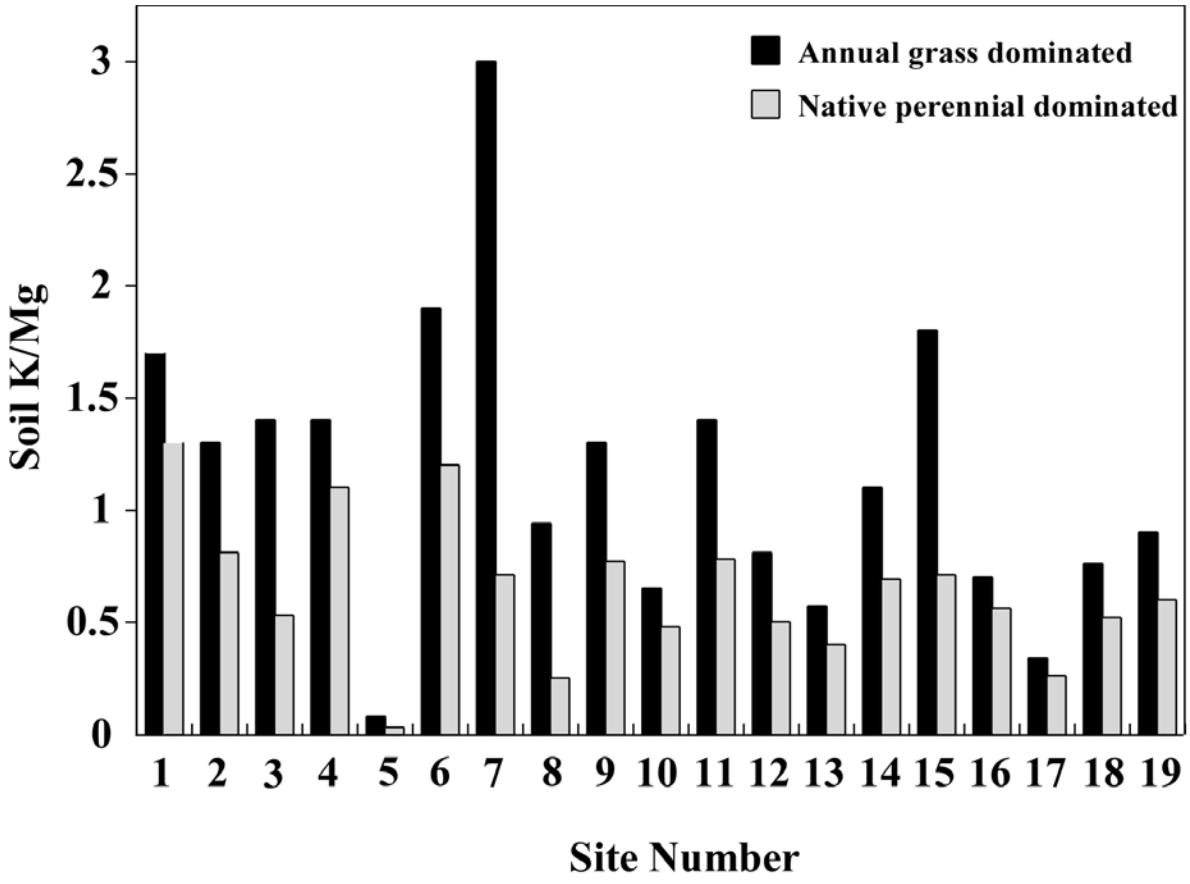

Figure 6. Comparison of sites with annual grasses and those without annual grasses in SE Utah. Note that sites with annual grasses consistently had higher K/Mg than sites without annual grass.

(total $R^2 = 0.73$). Sites at 500-950m were positively correlated with P/$CaCO_3$, K/Mg, and Cu (total $R^2 = 0.62$). For sites ranging from 950-1100 m there was only a very weak correlation between predicted annual grass cover and Mn ($R^2 = 0.08$). In contrast, annual grass cover at sites above 1100m elevation was positively correlated with P/$CaCO_3$, silt, average annual evapotranspiration and negatively correlated with Ca, clay, and altitude (total $R^2 = 0.91$).

Colorado Plateau: At the small scale (80 ha), invaded had higher K, K/Ca, K/Mg and CEC than uninvaded plots (Table 3). A linear regression analysis showed K and K/Mg best predicted annual grass cover ($R^2 = 0.66$ and 0.80, respectively). At the intermediate scale (8,000 ha), paired t-tests showed sites with annual grasses consistently had higher K and K/Mg than sites without annual grass (Figure 6). As with the smaller scale, there was no correlation with N or P and annual grass cover.

At the watershed level (80,000 ha), when all sites and all data were combined, negative predictor were % cover bare ground and the lichen *Collema*, whereas the positive predictor was K/Mg ($R^2 = 0.54$; Table 4). When we divided the sites into elevation classes, we got much better resolution. At sites with an elevation of less than 1400m, the driving variables of annual grass cover were positively correlated with soil depth, K/Mg, and P ($R^2 = 0.99$). However, as seen in the Mojave, higher elevation sites (>1400 m), P/CaCO3 and soil depth were positively correlated with annual grass cover ($R^2 = 0.41$). If sites above 1585 m were run separately, P/$CaCO_3$ was positively correlated with annual grass cover ($R^2 = 0.98$), indicating that the importance of P availability increased with elevation. It should also be noted that soils at higher elevations were slightly less sandy than those at lower elevations, which may have influenced these results (71 vs. 75%; Table 5).

We also employed a regression tree approach to the SE Utah sites. We did this in three ways. First, we included all the variables, as with the other deserts. This analysis explained 94% of the deviance, and 98% of the sites were correctly classified (Figure 7, Table 6). The most significant variable was P/Mn, and also included the surficial unit, elevation, aspect, heat load, parent material (Table 6), K/(Mg+Ca), total N, silt, coarse sand, Fe, and medium sand. In answer to our first management question "What could a manager say about annual grass distribution if they only had a soil survey, a geology map, and a topographic map?" the resultant tree used parent material for the first and largest division (Figure 8, Table 6). After that, the model used elevation, pH, all cations, soil texture, heatload, and CEC. Percent deviance explained by this analysis was 100%, with 100% of the sites correctly classified. For our second management question, we did not use the parent material information. Our classification rate was again 100%, with 100% of the sites correctly classified. The first division of this model was elevation, followed by texture, all cations, heat load, and CEC (Figure 9).

Great Basin: Stepwise regression of data from the Great Basin sites showed K and Mn were positively correlated and perennial grass, survey clay (obtained from the soil survey instead of analysis of collected soil), bioturbation, and pH were negatively correlated with annual grass cover ($R^2 = 0.73$; Table 7). We also desired a model that excluded all biotic variable (so annual grasses could be mapped from readily available data); with this model we found K and Mn positively correlated, and survey clay negatively correlated, with annual grass cover ($R^2 = 0.48$).

We also analyzed this data with a regression tree model. The main dividing factor was K, followed by P and elevation. Other factors in the tree were very fine sand, Ca, and total N. This model explained 99% of the variance (Figure 10).

Analysis of sites with and without annual grasses: We also compared a few key soil nutrients between the paired invaded and uninvaded sites that have been reported to influence annual grass invasion (Table 8). Unlike the stepwise regression and regression tree models, N and K were significantly higher in the invaded sites when compared to the uninvaded sites. For the Colorado Plateau sites at the landscape scale, only P was significantly higher in the invaded sites, although Mn and Zn tended to be higher as well. In the Great Basin, similar to the stepwise regression and regression tree models, P and Mn were significantly higher at invaded sites than uninvaded sites. Interesting, N and Zn were also higher in the invaded sites although they did not show up in the regression models.

	Needles		
	Predictor	**R^2**	**Correlation sign**
All sites	Bare ground	0.24	-
	K/Mg	0.41	+
	Collema cover	0.54	-
<1400 m	Soil depth	0.69	+
	K/Mg	0.94	+
	P	0.99	+
>1400 m	$P/CaCO_3$	0.29	+
	Soil depth	0.41	+
>1585 m	$P/CaCO_3$	0.97	+

Table 4. Results of a stepwise regression model for the Colorado Plateau sites at the watershed scale for all sites combined. Because we believed soil nutrients would vary with precipitation and thus elevation, we also grouped the sites into those <1400m and those >1400m.

		% Sand		% Clay		% Silt	
		mean	std. error	mean	std. error	mean	std. error
Mojave	200-500	75	2	12	1	12	1
	500-950	77	1	10	0	13	1
	>1100	70	2	12	1	17	2
	All	75	1	11	0	14	1
Co. Plateau	<1400	75	4	9	1	16	4
	>1400	70	1	14	1	16	1
	>1585	62	2	20	1	18	1
	All	70	1	14	1	16	1
Great Basin	<1400	45	3	17	1	38	3
	>1400	33	4	23	1	44	3
	All	36	3	22	1	42	2

Table 5. Comparison of soil texture in the different elevation groups used in the stepwise regressions.

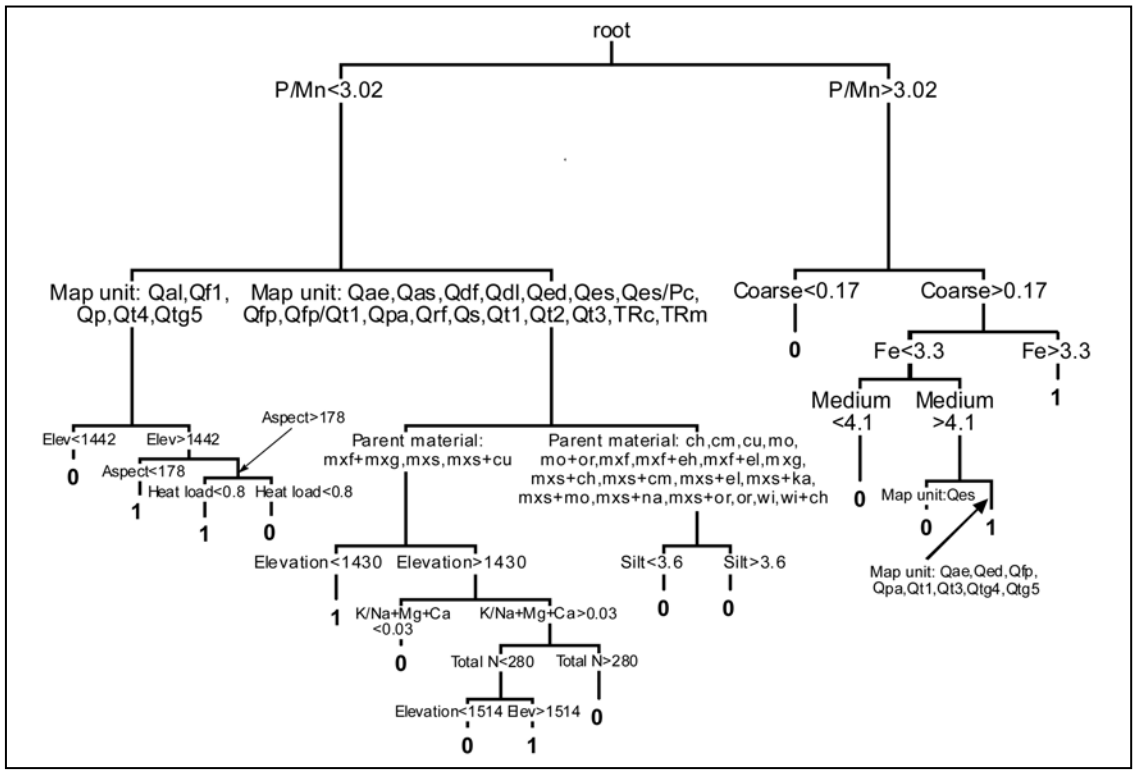

Figure 7. Regression tree analysis of the Colorado Plateau sites, using all the data available, to ascertain what factors best predicted the presence/absence of annual grass. Percent deviance explained was 94%, and 98% of the sites were correctly classified.

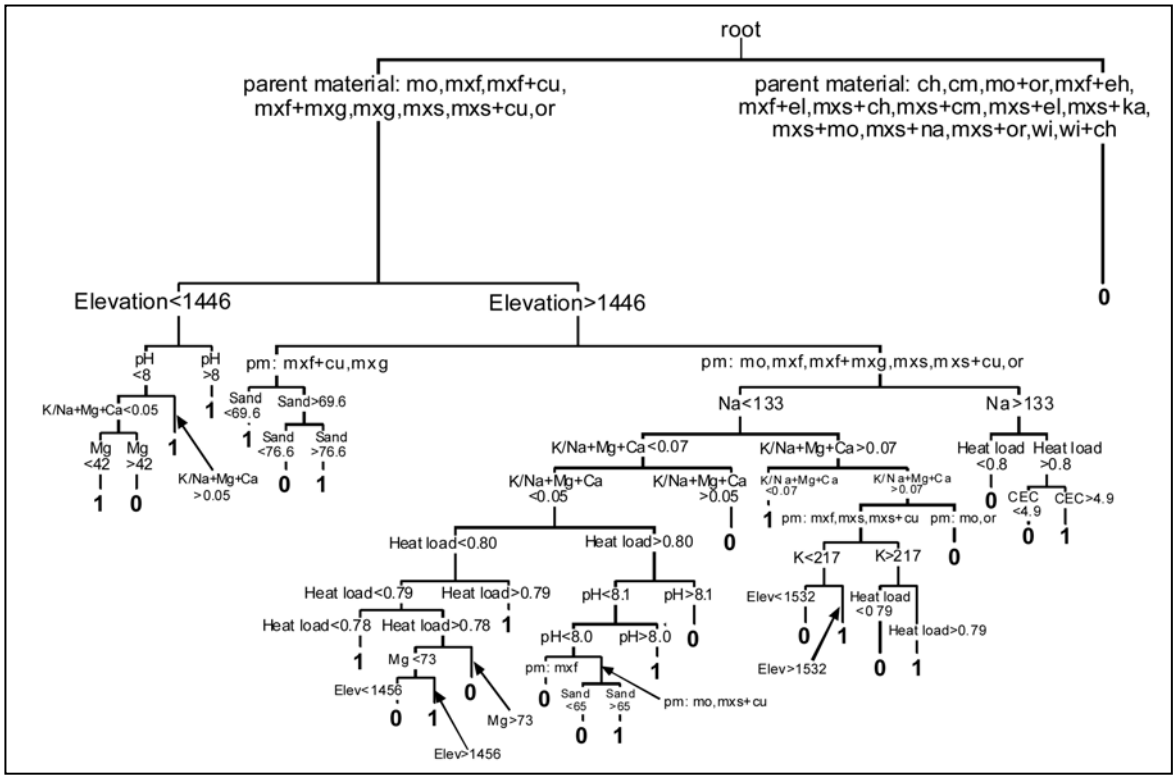

Figure 8. Regression tree analysis of the Colorado Plateau sites, using data available from a soil survey, a geology map, and a topographic map (i.e., parent material, K, Mg, Ca, Na, pH, CEC, soil texture, elevation, slope, aspect, heat load). Percent deviance explained by this analysis was 100%, with 100% of the sites correctly classified.

Key to parent material:

Abbrev.	Parent material	Texture
mxs	Mixed sands	Coarse
mxg	Mmixed gravels, mostly volcanic	Coarse
mxf	Mixed fines: sand and silt	Fine
mo	Moenkopi	Shale
or	Organ Rock	Shale
ch	Chinle	Shale
cm	Cedar Mesa	Coarse
na	Navajo	Coarse
ma	Mancos	Fine
cu	Cutler	Fine
el	Elephant	Fine
ho	Honaker	Fine
ka	Kayenta	Fine
wi	Wingate	Coarse

Key to surficial units:

Qaf	Artificial fill and quarries (Holocene)
Qs	Stream-channel alluvium (Holocene)
Qfp	Floodplain deposits (Holocene)
Qed	San dune deposits (Holocene)
Qrf	Rock fall debris (Holocene)
Qt1	Young terrace alluvial deposits (Holocene)
Qf1	Young alluvial fan deposits (Holocene)
Qr	Colorado River terrace deposits (Holocene)
Qp	Ponded deposits (Holocene)
Qes	Sand sheet deposits (Holocene)
Qf2	Young intermediate alluvial fan deposits (Holocene)
Qae	Alluvium and sand sheet deposits (Holocene)
Qal	Alluvial deposits (Holocene and Pleistocene?)
Qt2	Intermediate alluvial terrace deposits (Holocene and Pleistocene?)
Qt3	Old alluvial terrace deposits (Pleistocene)

Table 6. Definitions of the parent material and surficial unit codes for the Colorado Plateau regression trees.

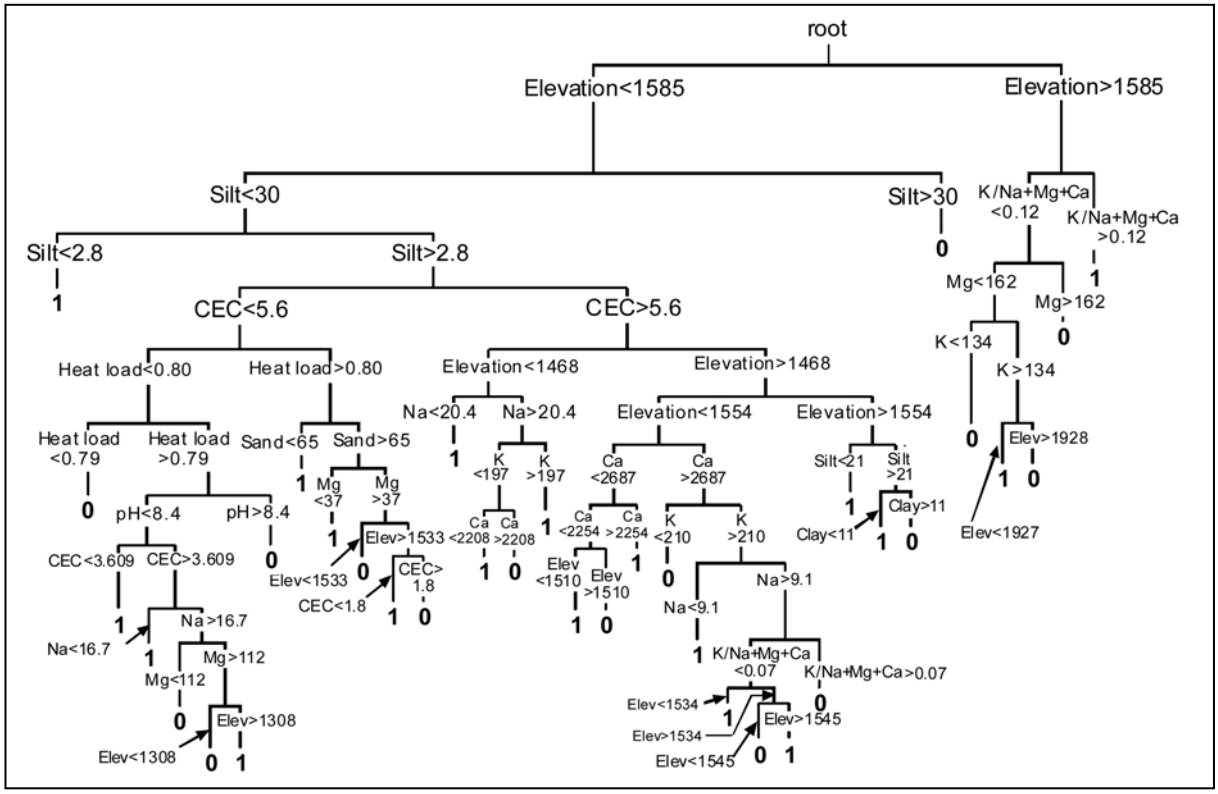

Figure 9. Regression tree analysis of the Colorado Plateau sites using only data from a soil survey and a topographic map (K, Mg, Ca, Na, CEC, pH, soil texture, elevation, slope, aspect, heat load). Percent deviance explained by this analysis was 100%, with 100% of the sites correctly classified. 0=<10% annual grass; 1=>10% annual grass.

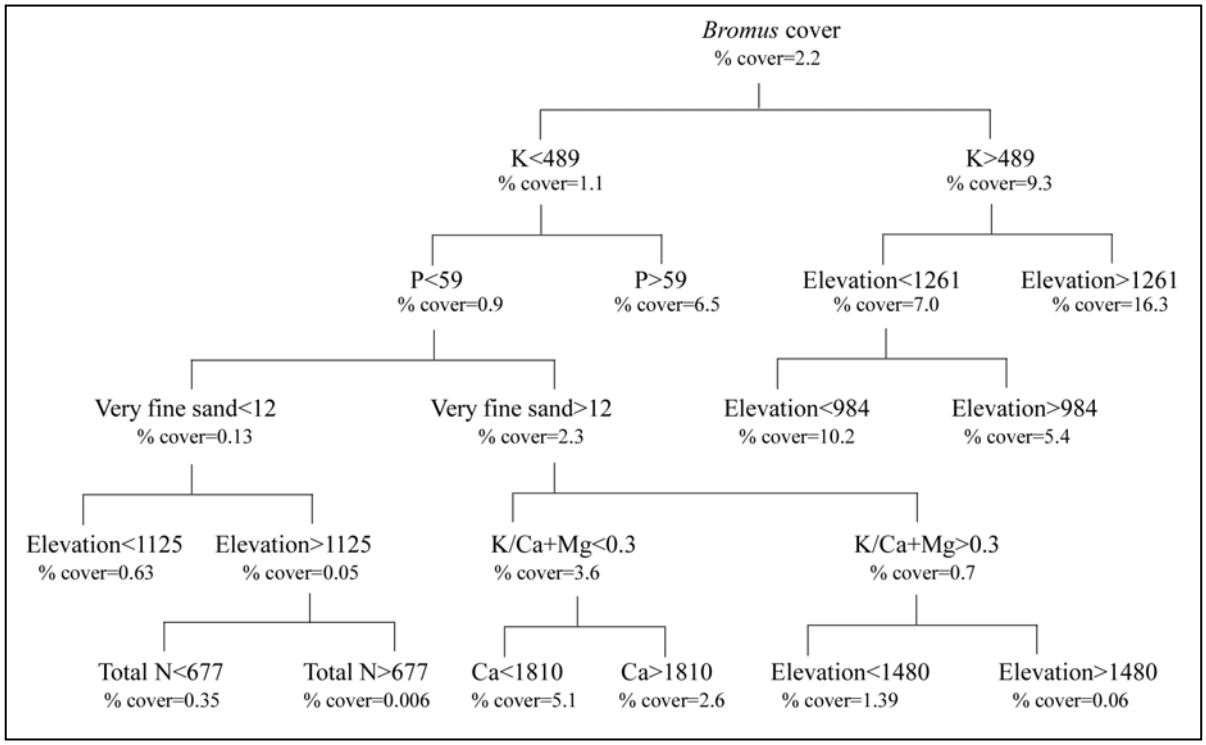

Figure 10. A regression tree model of the Great Basin sites. Percent variance explained by this tree is 99%.

Great Basin			
	Predictor	R^2	Correlation sign
Without biotic variables	K	0.24	+
	Clay	0.35	-
	Mn	0.48	+
With biotic variables	% Cover native grass	0.57	-
	% cover bioturbation	0.67	-
	pH	0.73	-

Table 7. Results of a stepwise regression model for the Great Basin for all sites combined. Unlike the Mojave and Colorado Plateau sites, grouping sites by elevation did not produce satisfactory results.

		With annual grass		Without annual grass		
Desert	**Variable**	**mean**	**std. err.**	**mean**	**std. err.**	***p***
Mojave	N	315 ±	26	187 ±	29	0.01
	P	6.4 ±	0.4	5.8 ±	0.5	0.38
	K	180 ±	10	230 ±	17	0.01
	Mn	3.6 ±	0.2	3.0 ±	0.4	0.19
	Zn	0.3 ±	0.0	0.3 ±	0.0	0.43
Co Plateau	N	311 ±	32	420 ±	81	0.20
	P	7.7 ±	0.5	6.0 ±	0.6	0.04
	K	172 ±	13	151 ±	9	0.21
	Mn	4.4 ±	0.4	5.6 ±	0.6	0.09
	Zn	0.4 ±	0.1	0.6 ±	0.1	0.06
Great Basin	N	1763 ±	239	1135 ±	104	0.01
	P	40.7 ±	4.0	31.3 ±	3.7	0.02
	K	491 ±	29	431 ±	40	0.17
	Mn	53 ±	9	39 ±	8	0.01
	Zn	3.1 ±	0.5	2.0 ±	0.3	0.003

Table 8. Pairwise comparisons of a few selected nutrients showed P, N, K, Mn, and Zn were higher in the invaded sites than the uninvaded sites.

Discussion

Our results show that soil characteristics were generally the most important in distinguishing invaded patches from uninvaded patches in all the deserts surveyed. Differences among species in the rate and ratio of resource use can be important at the population and community level of organization (Tilman 1988). Differences are also important at the ecosystem level because they imply differences in the ratio of elements in plant tissue and therefore affect nutrient cycles (Vitousek 1993). Our results show that P, P/$CaCO_3$, K, and K/Mg were consistently important in predicting where annual grasses occur in western US deserts.

P as a limiting nutrient: In the alkaline, high Ca soils that dominate most deserts, P availability to plants is typically low due to the following interrelated geochemical factors: (1) P sorption reactions with carbonate minerals such as $CaCO_3$, (2) the precipitation of sparingly soluble calcium phosphate compounds, and (3) the presence of high Ca and HCO levels which inhibit the dissolution of carbonate and Ca-P compounds due to common-ion effects and the neutralization of biogenic acids generated to enhance P bioavailability (Barber 1995, Marschner 1995, Frossard et al. 1995). Rhizosphere acidification due to the combined activities of roots, mycorrhizal symbionts and associated rhizosphere microbes is a common means by which nutrient dissolution and acquisition can be enhanced in calcareous soils (Marschner and Romheld 1996, Hinsinger 1998). Rhizosphere acidification most often is caused by protons excreted to balance uptake of cation as such as NH_4 and Ca (e.g., Grinsted et al. 1982, Hedley et al. 1982, Bekele et al. 1983, Gillespie and Pope 1990), but respiratory CO_2 can also be an important acidification mechanisms through its reaction with H_2O to form carbonic acid (Danin 1983, Jurinak et al. 1986, Hinsinger 1998). Because annual plants generally have a higher nutrient demand than perennials, it is likely that annual grasses would show a P limitation before the native perennial plants. Indeed, a study in SE Utah showed that *Bromus* tissue P was lower than optimal (Epstein 1961, Miller 2000). Schlesinger et al. 1989 inferred that vegetative differences between contrasting soils in their study were due to the effects of Ca and HCO on P availability to plants. DeLucia et al. (1989) found that Bromus tectorum was P-limited in hydrothermally altered soils possessing $NaHCO_3$-extractable P levels compared to those found in the SE Utah study (Miller 2000). Wright and Mooney (1965) also found plants growing on high pH dolomite soils were P-deficient and Billings (1950) found low P and high Ca to limit sagebrush distribution. Parker (1995) suggests that P may affect the distribution of different plant species on alluvial fans in the Sonoran desert.

Climate can affect the solubility of $CaCO_3$, and thus the availability of P to plants. The generation of H_2CO_3 in the soil environment depends on 1) the partial pressure of CO_2, 2) soil water content, and 3) CO_2 solubility in H_2O (Krasuskopf and Bird 1995). The solubility of CO_2 in H_2O, like that of other gases, is greater at cold temperatures than at warm temperatures. Thus, all else being equal, H_2CO_3 formation in the soil environment can be conceptualized as the interaction between biotic CO_2 production and abiotic CO_2 solubility. Both of these vary temporally in relation to soil temperature and soil moisture, but they vary opposite one another in relation to these conditions. A transient maximum (Seastedt and Knapp 1993) in H_2CO_3 production should therefore occur when the curve of increasing CO_2 production and the curve of decreasing CO_2 solubility intersect along a temporal environmental gradient of increasing soil temperature and decreasing soil moisture. To the degree that H_2CO_3 generation enhances nutrient solubility in calcareous soils (e.g., P), a transient maximum (or multiple transient maxima) in nutrient bioavailability likewise should correspond with the temporal peal (or peaks) in H_2CO_3

generation. *Bromus* exhibits considerable below-ground winter growth when soils are cold and moist (Harris 1967), presumably increasing respiratory CO_2 production, enhancing rhizosphere H_2CO_3 generation, and facilitating the dissolution and acquisition of carbonate-bound nutrients (Figure 11). Data from in-situ resin bags in SE Utah are consistent with the hypothesis that nutrient solubility should increase during cold, moist conditions (Miller 2000). In-situ adsorption rates for most mineral ions were highest in winter, although it was not possible to distinguish between specific effects of H_2CO_3 and general effects of sustained, moist conditions. In situ resin bag P concentrations peaked during this time as well. Lajtha and Schlesinger (1988) found that in-situ resin bag P concentrations peaked during the cool winter period in the Chihuahuan desert and that laboratory extractions done at 4 ^oC recover significantly more P than those done at 25 ^oC (Magid and Nielsen 1992). Although diffusion rates of solution-phase ions decrease with decreasing temperature, effective P diffusion in calcareous soils may actually increase with decreasing temperatures above freezing because H_2CO_3 generation facilitates carbonate dissolution and the transition of solid-phase P to solution-phase P (Jungk and Claassen 1997). *Bromus* growth rates were greatest in winter, and were positively correlated with K and P/Ca and

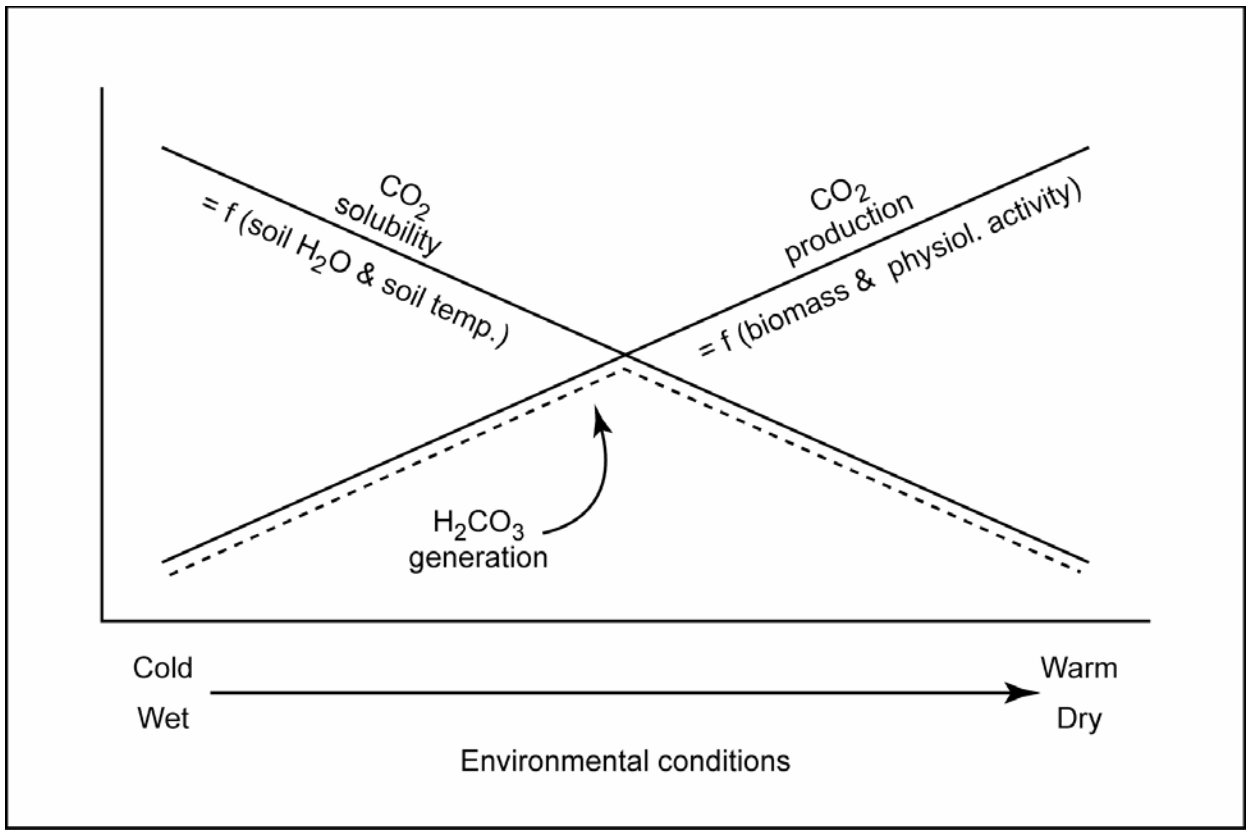

Figure 11. A conceptual model of P availability as driven by temperature.

inversely with ANP.

Therefore, one would expect that P would be most limiting in soils with high pH, Ca, or

$CaCO_3$ when occurring in regions with low winter precipitation (low elevations with summer precipitation) or where winter temperatures stay very high (low elevations) or very low (high elevations). Our sites occurred along a gradient of winter precipitation: Chihuahuan < Mojave < Colorado Plateau < Great Basin (Figure 12**)**. Our results show that where winter precipitation is low (Chihuahuan and Mojave deserts), P limitations reduce annual grass occurrence (and to such a degree in the Chihuahuan that annual grasses are excluded). Low winter temperatures (high elevations) also result in a P limitation. As total winter precipitation increases (going northward to the Colorado Plateau and the Great Basin), K becomes the limiting nutrient (see below).

K as a limiting nutrient: Less work has been done with K as a limiting nutrient in dryland soils than P as a limiting nutrient. Plant species differ in their ability to take up K, and this is positively and highly correlated with their root cation exchange capacity (CEC; $R^2 = 0.77$ as reported in Crooke and Knight 1962; Gray et al. 1953). Root CECs of annual grasses are generally 2-5x higher than associated native grasses (Belnap et al., unpub). Annual grasses also have much higher tissue concentrations of K than adjacent native grasses (Belnap et al., unpub.) and other plants (Blank 2002), which may indicate that annual grasses have a higher requirement for K than the native grasses (Tilman 1982).

Increased levels of tissue K (above deficiency levels) can increase performance measures, such as grain yield, in plants (Raman et al. 1986). Tilman et al. (1999) also report K to be limiting for

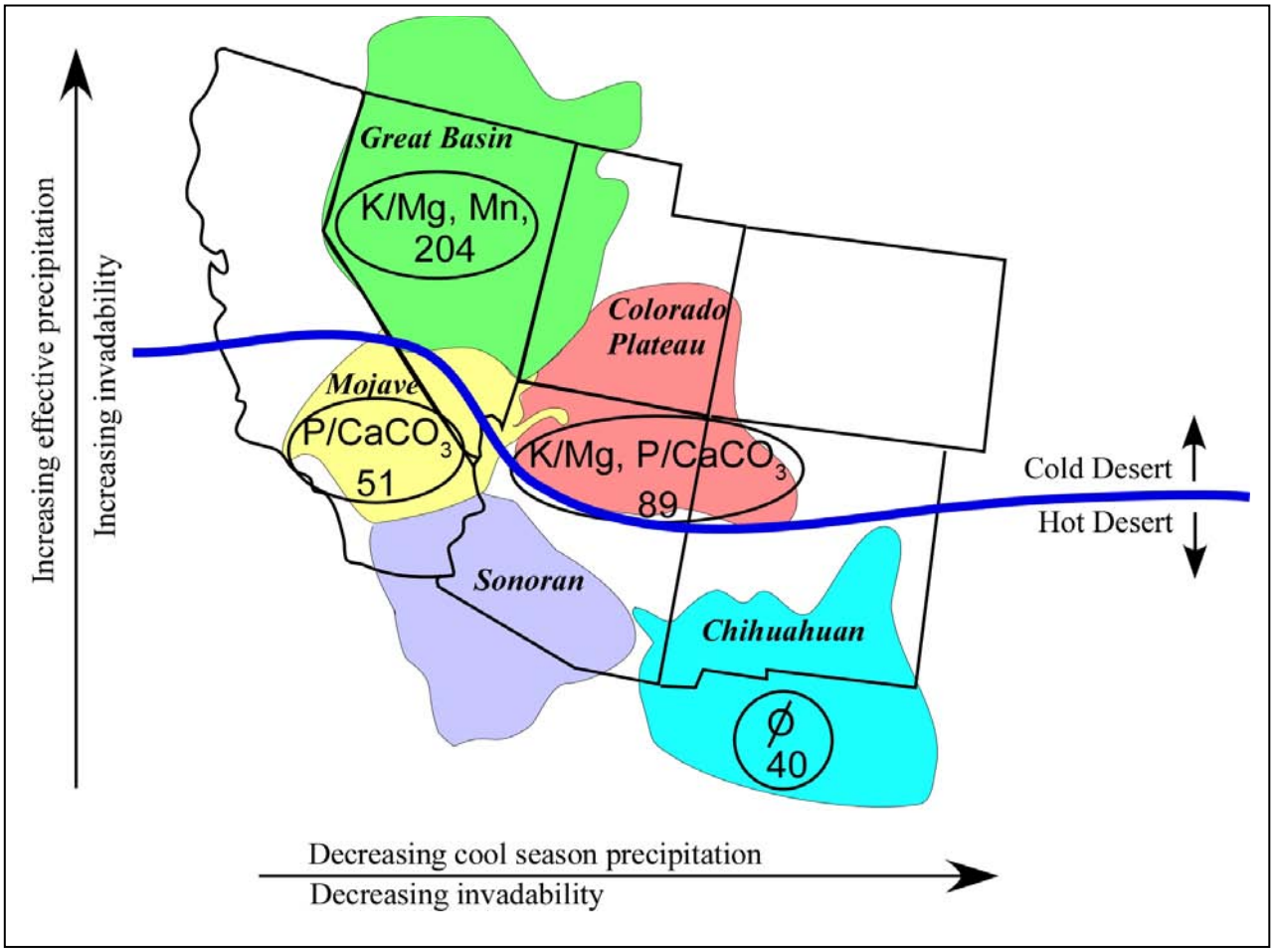

Figure 12. A conceptual model of nutrients limiting annual grass cover and distribution in SW deserts of the United States. Numbers represent the amount of precipitation, in mm, that falls annually when air temperatures are below 10 ^{o}C, which we suggest controls phosphorus availability in desert soils (see text for a more detailed explanation).

Taraxacum in the field.

K also interacts with other cations that may explain its importance to annual grasses. First, K mediates plant osmoregulation (Maser et al. 2002, Wang et al. 2002). The presence of high Na can be toxic to many plants, and there are multiple studies showing that K ameliorates Na toxicity in plants (e.g., Kaya et al. 2002, Maser et al. 2002, Golldack et al. 2003, Zeng et al. 2003) and other organisms such as bacteria (e.g., Kraegeloh and Kunte 2002). The transport of K over Na is especially pronounced in actively photosynthesizing organisms such as young leaves and developing seeds (Wang et al. 2002). However, the extent to which plants utilize K to avoid Na stress varies among species (Maser et al. 2002). Secondly, K has also been implicated in plant avoidance of water stress (Xu et al. 2002).

Crooke and Knight (1962) and Scott and Billings (1964) were the first to note that soils with high K/Mg ratios were dominated by annual plants, whereas perennial plants dominated soils with lower K/Mg ratios. This finding was followed up by Harner and Harper (1973), Pederson and Harper (1979), Woodward et al. (1984) and McKnight et al. (1990) to explain patterns of plant distribution in natural vegetation in the arid western US. Other studies also support the observations that high levels of Mg and Ca can restrict plant uptake of K in both the laboratory and the field (Kahn and Hanson 1957, Epstein 1961, Elzam and Hodges 1967, Maas 1969, Garcia et al. 1999, Sinanis et. al 2003).

The mechanism for these findings is still under investigation. The above authors suggest that because annual plant roots generally have a higher CEC than perennial plant roots (Heintze 1961) the more highly-charged roots attract higher-charged polyvalent cations (Mg, Ca) more efficiently than lesser-charged monovalent cations (K, Na; Smith and Wallace 1956). Roots neutralized with polyvalent cations would be less capable of attracting monovalent cations and thus would be at a competitive disadvantage in soils with low monovalent/polyvalent ratios. Therefore, soils with high mono/polyvalent (K/Mg) cation ratios should favor plants with higher root CECs (annuals) over those with lower root CECs (perennials), while soils with low ratios should favor perennials over annuals.

Micronutrients and CEC: Micronutrients are seldom considered in studies of plant distribution. However, we have consistently found that micronutrients are important in predicting the distribution of disparate organisms such as soil lichens, annual grasses, and perennial shrubs. There is very little information on what role they may be playing, although Zn, Mn, and Fe can form reactive oxides that bind with P, making it plant-unavailable. In this study, annual cover was negatively correlated with P/Mn, Zn, and Fe, indicating such bonding may be occurring. However, there are also instances where the relationships between plants and micronutrients are positive (e.g., in this study, the relationship with Mn and Cu was positive in some instances), indicating there are places where these micronutrients may be limiting.
This may be due to the fact these micronutrients can complex with carbonates, and thus become unavailable to plants.

Soil cation exchange capacity is a measure of how strongly the soil holds nutrients, thus competing with plants and microorganisms for these nutrients. As would be predicted, when CEC appeared in the regression, it was negatively correlated with annual grass cover.

Why not N? It is very interesting that we did not find N to be the driving variable for explaining the distribution of annual grasses using regression models in any of the regions we sampled (although N did show up at the bottom of two regression trees). Multiple studies (e.g., Stohlgren et al. 1999, 2001; Stohlgren 2002; Ehrenfeld 2003; Heady et al. 1992; Hoopes and Hall 2002) report that invasions occur into habitats that are higher in N than nearby non-invaded

habitats. The lack of importance of N in our studies may be explained in several ways. First, the fact that N did not appear in the regression analyses did not mean it was not significantly different between uninvaded and invaded sites in some locations. For instance, our paired sites in the Great Basin showed N was 55% higher in the invaded patches than the paired adjacent uninvaded sites. However, in relation to the other nutrient differences, N did not show up as an important factor in the regression analyses. Secondly, P is often not measured in studies and thus while N may appear to be the driving variable in these studies, the importance of P may be missed. Thirdly, N may be more of a driver in regions with higher precipitation, whereas this study focused on lower elevation dryland sites. For instance, at our low precipitation sites, correlation analyses did not find any relationship between annual grass cover and N (although the paired tests showed a significant difference), whereas at our higher precipitation Great Basin sites, we did find such a relationship, albeit minor.

Factors that influence moisture availability: Many factors influence soil moisture and appeared as important drivers of annual grass cover, including aspect, heat load, elevation, and evapotranspiration. Heat load is a combination of slope, aspect, and elevation. Because they are autocorrelated, only heat load was used in the stepwise regression analyses. However, regression trees do not require independent variables. Therefore in the regression trees where all three factors were identified as drivers (e.g., Colorado Plateau, Figs. 7-9), it is clear that soil moisture is very important in controlling annual grass distribution. This is consistent with the fact that *Bromus tectorum*, the annual grass found at this site, is at the southern end of its range due to moisture constraints. Although soil texture appeared important at the Colorado Plateau and Great Basin sites with some of the analyses, it was much less so for the Mojave sites.

The nature of the parent materials and surficial units influence soil texture, which in turn influences soil moisture availability. (It should be noted that these three factors also influence soil chemistry and CEC, discussed in the sections above). Sandy soils tend to let water drain to deeper levels, where it is available during drier times if the plants are capable of rooting at depth. Silt and clays have a higher water-holding capacity and tend to hold water up higher in the soil profile. At the Colorado Plateau sites, most annual grasses were found on parent materials that weather to fine-textured soils or were mixed gravels (Table 6), again indicating that annual grasses in this area are moisture-limited. However, fine-textured soils are also more nutrient-rich than sandy soils, and so this observation may easily be confounded by soil nutrient status.

Soil texture may have influenced the results we obtained when we compared the different regions. Although the Mojave and Colorado Plateau sites had very similar texture, both regions showed a decrease in sand and an increase in clay and silt with elevation. In addition, the Great Basin sites were far less sandy than the Mojave or Colorado Plateau sites. The effect of texture appeared in the higher elevation Mojave sites and the Great Basin sites, as well as the regression trees for the Colorado Plateau sites. However, it was never the most significant variable.

How do we know that the observed patterns are not a results of annual grasses altering soil chemistry after invasion?

The observed patterns could have certainly be a result of the invasion, rather than predicating an invasion, as annual grasses are known to alter soil nutrients. However, we have several lines of evidence to suggest that this is not the case at least in the lower elevation Colorado Plateau sites. At the small scale sites, soil chemistry was measured in 1964, over 30 years before the invasion. When current annual grass cover was regressed against 1967 soil chemistry at the same sites, there was no correlation with N or P, but a correlation of 0.65 ($p < 0.01$) with K. (Mg was not measured in 1967, and so we could not analyze K/Mg). Nutrients

have been analyzed annually for the six years after the invasion. Although *Bromus* appears able to affect levels of available P in the soil, this effect appears to be seasonal (winter only) and only during wet years (this report, Section IV, Part 3). Other studies in this same area show that while Bromus invasion can also affect soil N, this affect is minor over the long-term (this report, Section IV, Part 5). Other nutrients such as K and Ca show no change at sites with *Bromus* when compared to uninvaded soils. Unfortunately we have no information on soils before the invasion at the other Colorado Plateau sites, or the sites in the other three deserts.

Conclusion

Soil chemistry appears to be the most important variable in predicting annual grass cover. Because this is a mappable variable, we now have the power to spatially display both invaded sites and those vulnerable to invasion. However, it should be kept in mind that at sites where P availability is the controlling variable, alterations in climate is expected to alter invadability by annual grasses. In addition, these results should be corroborated with experimental manipulations. Our analysis of the data from a manager's perspective showed that information in soil surveys and geology maps can be a powerful tool in predicting annual grass cover.

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Section III: Can soil factors that confer resistance be used to suppress *Bromus* while not affecting the germination or success of native plants?

Laboratory studies: soil amendments that suppress *Bromus* emergence

The objective of this study was to identify soil additives that allowed germination but inhibited emergence of *Bromus tectorum*, while not affecting germination or emergence of the native perennial grass *Hilaria jamesii*. Based on data from previous studies that *Bromus* was stimulated by soil nitrogen (N), phosphorus (P), and /or potassium (K), we focused on altering these nutrients. Most water-soluble treatments we added inhibited *Bromus* germination and/or emergence. We attribute the inhibitory effects of these treatments to excessive salinity and ion-specific effects of the additives themselves. An exception to this was oxalic acid, which showed no effect on *Bromus*. Most water-insoluble treatments had no effect in soils with high P, but did have an effect in soils with low P. Zeolite was effective regardless of P level, probably due to the high amounts of Na^+ it added to the soil solution. Most treatments at higher concentrations resulted in lower *Bromus* emergence rates when added to soils currently dominated by *Bromus* than when added to soils from uninvaded (but theoretically invadable) *Hilaria* soils. This difference is possibly attributable to inherent differences in labile soil P.

In *Stipa* soils, considered uninvadable by *Bromus*, additions of high amounts of N resulted in lower emergence. This may have been an effect of NH_4^+ interference with uptake of K and/or other cations, or toxicity of high N. We also saw a positive relationship between *Bromus* emergence and pH in *Stipa* soils. *Hilaria* development parameters were not as susceptible as *Bromus* to the treatments, regardless of concentration. Our results suggest that there are additions that may be effective management tools to inhibit *Bromus* in calcareous soils, including 1) high salt applications, 2) K-reducing additions (e.g., Mg), and/or 3) P-reducing additions.

We then grew *Bromus* and *Hilaria* alone and together in each of nine soil treatments that manipulated levels of soil phosphorus and potassium. *Hilaria* showed no biomass decline with any of the applied treatments when grown in monoculture or in combination with *Bromus*. However, *Hilaria* biomass in the combination pots was reduced by 50% or more relative to the monoculture pots. In contrast to *Hilaria*, most treatments (except CaO) reduced *Bromus* biomass when grown in monoculture. However, in the combination pots, the presence of *Hilaria* in the pots with *Bromus* ameliorated the negative effect of the treatments and *Bromus* biomass showed no declines with our amendments. In fact, *Bromus* biomass was enhanced by up to 400% when grown with *Hilaria*, indicating that the presence of the native grass facilitated growth in *Bromus*. This may be explained by root CEC: as expected when comparing an annual with a perennial grass, *Bromus* had much higher root CEC than *Hilaria*, and *Bromus* tissue concentrations for all elements were higher in *Hilaria* except for Na and Mn. All treatments except CaO (the treatment that did not suppress *Bromus* biomass) increased Na uptake in *Bromus*. However, tissue Na in *Bromus* was always lower than that of *Hilaria*, indicating *Bromus* is better able to discriminate against this element. Combined with findings from other studies, we hypothesize that *Bromus* is more negatively impacted by high soil salt levels than *Hilaria*.

We also speculate that the observed facilitation of *Bromus* by *Hilaria* and the suppression of *Hilaria* by *Bromus* is likely a result of either 1) *Bromus* tapping into *Hilaria's* mycorrhizal network, thus gaining access to water and nutrients that *Hilaria* would otherwise receive or 2) *Hilaria* roots exuding compounds that benefit *Bromus*. This would also include water and

dissolved nutrients made available by hydraulic redistribution of *Hilaria*. Because *Bromus* roots have a much higher CEC relative to *Hilaria* roots, *Bromus* would likely be able to outcompete *Hilaria* for any nutrients released into the soil. In summary, land managers are unlikely to ever extirpate *Bromus*. Adding high levels of salt to the soils when restoring areas may assist native reestablishment by temporarily suppressing *Bromus*. However, the presence of natives is likely to favor the continued presence of *Bromus* by facilitating *Bromus* growth.

Results from these laboratory experiments were then used to design field experiments. First, we conducted a reciprocal soil transplant experiment to determine whether microhabitat or soil chemistry explained the observed pattern of *Bromus* in *Hilaria*-dominated areas. Emergence and biomass of *Bromus* was similar regardless of whether soil was in the *Hilaria* or *Stipa* sites; however, emergence was higher in soils that originated in *Hilaria* sites suggesting that soil chemistry explains *Bromus* invasion patterns.

Second, we investigated soil amendments that had been successful in the laboratory at allowing *Bromus* germination but reducing emergence without having negative effects on *Hilaria*. We conducted experiments in two different years where we applied four amendments ($CaCl_2$, $MgCl_2$, NaCl and zeolite) at various concentrations to reduce available P and K. No amendments negatively affected *Hilaria* biomass, but NaCl slightly reduced emergence. All amendments except 4x $CaCl_2$ and 0.5x zeolite negatively affected *Bromus* emergence and/or biomass; however, amendments did not always affect emergence and biomass similarly. In addition, amendment effectiveness depended on amendment concentration and year of application. In some cases, the effects of amendments changed over time where emergence and/or biomass was first depressed and then there was no effect or a stimulatory effect. Zeolite (1x) had the strongest negative effect on *Bromus* with little effect on *Hilaria*. In a laboratory experiment, zeolite significantly increased Zn, Fe, Mn, Cu, exchangeable Mg, exchangeable K, exchangeable Na and NH_4 while decreasing Ca in the soil. Our results reveal several possible amendments to control *Bromus.* However, these same amendments can stimulate emergence and/or biomass in later years. Variability in effectiveness due to abiotic factors such as precipitation and soil type must be accounted for when establishing management plans.

Can soil factors that confer resistance be used to suppress *Bromus* while not affecting the germination or success of native plants?

- There are soil amendments that successfully suppress *Bromus*, yet had little effect native plants. These additives exploit the fact that *Bromus* appears salt-sensitive whereas native grasses are salt-tolerant.
- However, there is evidence that the effect of the tested amendments in the field change with precipitation regimes and over time, and amendments that suppressed *Bromus* in one year can actually stimulate it the next year. Therefore, before any of these amendments are used, long-term experiments are needed.
- The presence of natives stimulates the growth of *Bromus*. Thus it is unlikely we will ever extirpate *Bromus* from US rangelands. Instead, we need to focus on assisting native plant establishment and continued success within invaded sites.

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Effects of soil amendments on germination and emergence of downy brome (*Bromus tectorum*) and *Hilaria jamesii*

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Downy brome is an introduced Mediterranean annual grass that now dominates millions of hectares of western U.S. rangelands. The presence of this grass has eliminated many native species and accelerated wildfire cycles. The objective of this study was to identify soil additives that allowed germination but inhibited emergence of downy brome, while not affecting germination or emergence of the native perennial grass *Hilaria jamesii.* On the basis of data from previous studies, we focused on additives that altered the availability of soil nitrogen (N), phosphorus (P), and potassium (K). Most water-soluble treatments inhibited downy brome germination and emergence. We attribute the inhibitory effects of these treatments to excessive salinity and ion-specific effects of the additives themselves. An exception to this was oxalic acid, which showed no effect. Most water-insoluble treatments had no effect in soils with high P but did have an effect in soils with low P. Zeolite was effective regardless of P level, probably due to the high amounts of Na^+ it added to the soil solution. Most treatments at higher concentrations resulted in lower downy brome emergence rates in soils currently dominated by downy brome than in uninvaded (but theoretically invadable) *Hilaria* soils. This difference is possibly attributable to inherent differences in labile soil P. In *Stipa* soils, where *Stipa* spp. grow, but which are generally considered to be uninvadable by downy brome, additions of high amounts of N resulted in lower emergence. This may have been an effect of NH_4^+ interference with uptake of K or other cations or toxicity of high N. We also saw a positive relationship between downy brome emergence and pH in *Stipa* soils. *Hilaria* development parameters were not as susceptible to the treatments, regardless of concentration, as downy brome. Our results suggest that there are additions that may be effective management tools for inhibiting downy brome in calcareous soils, including (1) high salt applications, (2) K-reducing additions (e.g., Mg), and (3) P-reducing additions.

Nomenclature: Downy brome, *Bromus tectorum* L. BROTE; *Hilaria jamesii* L., galleta grass; *Stipa* spp.

Key words: Annual invasive grass, desert grasslands, semiarid, soil amendments.

Native North American ecosystems that have been invaded by the Eurasian–Mediterranean annual grass downy brome show critical alterations in ecosystem structure and function (see reviews in Mack 1981; Upadhyaya et al. 1986). Replacement of native vegetation and elevated wildfire frequency have reduced native plant and animal biodiversity, deteriorated agricultural and range lands, and required large expenditures for fire suppression (Vail 1994; Whisenant 1990). Downy brome invasion also has transformed soils, including food web structure, biogeochemical characteristics, and nutrient cycles (Belnap and Phillips 2001; Evans and Belnap 1999; Wilson et al. 1966). Continued downy brome dominance is encouraged through the positive feedback between this species and associated ecosystem alterations (Belnap and Phillips 2001; Evans et al. 2001). Consequently, land managers throughout the western United States need ways to prevent downy brome invasion or to restore invaded landscapes.

Semiarid grasslands in southeastern Utah, United States, that are dominated by *Hilaria jamesii* appear particularly susceptible to downy brome invasion. However, those dominated by needle-and-thread (*Stipa comata* Trin. & Rupr.) or *Stipa hymenoides* (Welsh et al. 1993) exhibit little, if any, invasion by downy brome (Belnap and Phillips 2001). Both downy brome and *Hilaria* occur in soils with higher exchangeable potassium (K) and silt than in areas where *Stipa* spp. dominate, suggesting that low K or water may limit this annual grass (Hansen 1999; Howell 1998). Downy brome growth in the field is also positively associated with the high ratio of soil K or phosphorus (P) relative to calcium carbonate ($CaCO_3$) and magnesium (Mg) or iron (Fe) oxides (Belnap and Phillips 2001; Miller 2000). These latter compounds can bind with P, rendering it unavailable to plants. In addition, Mg can inhibit K uptake (Haynes and Goh 1978; Thompson and Troeh 1978). Mg, Fe, and calcium (Ca) can also increase soil acid–neutralizing potential (ANP) or buffering capacity, which through sorption reactions may inhibit the availability of carbonate-related nutrients such as P, manganese (Mn), and copper (Cu) (Miller 2000). Combined, these data suggest downy brome is limited by K or P (or both) in these soils.

Howell (1998) and Morrison (1999) added magnesium oxide (MgO) and K to soils seeded with downy brome in greenhouse experiments and observed that Mg additions depressed and K additions stimulated downy brome emergence and biomass. Miller (2000) also observed that MgO additions in the field diminished downy brome establishment. Nitrate (NO_3^-) and ammonium (NH_4^+) have also been ob-

TABLE 1. Characteristics of soils from three different plant communities in southeastern Utah.

	Soil type		
	Stipa	*Hilaria*	*Bromus*
P (ppm)	7.3	9.1	17.1
Available K^+ (ppm)	70.4	179.2	198.4
Exchangeable Ca^{2+} (ppm)	2820.0	3174.0	2568.0
Exchangeable K^+ (ppm)	95.9	293.2	295.0
Exchangeable Mg^{2+} (ppm)	54.6	132.3	129.4
Exchangeable K^+/Mg^{2+}	1.5	2.2	2.2
Exchangeable Na^+ (ppm)	51.0	60.9	40.0
Organic matter (%)	0.3	0.3	0.4
Electrical conductivity (dS/M)	0.5	0.5	1.1
pH	8.0	8.2	7.8
Sand (%)	72.0	65.3	71.6
Silt (%)	18.1	17.4	14.1
Clay (%)	9.9	17.3	14.3
Total N (ppm)	89.3	87.4	73.9
NH_4-N (ppm)	4.1	6.5	7.4
NO_3-N (ppm)	1.6	1.6	19.6
$CaCO_3$ (%)	6.8	5.2	3.2
Cu^{2+} (ppm)	0.2	0.7	0.6
Fe^{2+} (ppm)	2.9	3.5	3.7
Mn^{2+} (ppm)	2.5	6.1	4.6
Zn^{2+} (ppm)	0.2	0.3	0.3

served to stimulate seed germination of many species (Egley and Duke 1985; Karssen and Hilhorst 1992).

The effects of pH on germination potential differ among plant species. Some species benefit from more acidic conditions, others prefer neutral or alkaline pH, and some show no response to pH manipulations (Justice and Reece 1954; Pierce et al. 1999; Susko et al. 1999). Data addressing the effects of pH on the germination of species on calcareous soils are generally lacking (Baskin and Baskin 1998), although one study demonstrated that acidic soils inhibit both germination and seedling growth of species that prefer calcium-rich soils (Okusanya 1978).

One managerial approach to diminishing the ecological success of invasive downy brome is to apply soil treatments that allow downy brome seeds to germinate but reduce or eliminate their emergence without also suppressing the germination and emergence of the native perennial grass *Hilaria*. Based on the literature reviewed above, we manipulated the availability of soil P, K, and nitrogen (N) and pH to determine if soil amendments could achieve this objective.

Materials and Methods

We collected downy brome seed in September 1997 from Canyonlands National Park (CNP), Needles District, southeastern Utah, United States (~1,500 m elevation; average annual precipitation and temperature 216 mm and 12 C, respectively; Miller 2000). In January 2000 we obtained *Hilaria* seed[1] that was grown nearby in Dolores, CO. Three sandy loam soils (Typic Torripsamments from the Begay series) dominated by different plant communities were collected at the Squaw Flat site of CNP (Table 1). "Downy brome soils" are previously *Hilaria*-dominated soils that have been dominated by downy brome for over 50 yr. "*Hilaria* soils" are uninvaded soils dominated by *Hilaria*, and "*Stipa* soils" are uninvaded soils dominated by *S. hymenoides* and needle-and-thread. Although *Hilaria* soils are considered invadable by downy brome, the soils we used supported no or small downy brome populations. To date, *Stipa* soils have been observed to be mostly noninvadable by downy brome.

The following methods were employed for soil analyses: P (Olsen et al. 1954) and available K (Schoenau and Karamonos 1993) were extracted with $NaHCO_3$. All exchangeable nutrients were extracted with ammonium acetate ($NH_4C_2H_3O_2$; Thomas 1982). Organic matter (OM) was determined by the Walkley–Black (1934) procedure. Electrical conductivity (EC) and pH were determined using a saturated paste (Rhoades 1982). Texture was determined by the hydrometer method and total N by Kjeldahl analysis (Bremner 1996). Inorganic N was extracted with KCl and analyzed by steam distillation (Kenney and Nelson 1982). $CaCO_3$ was measured by HCl neutralization (Allison and Moode 1965) and thus includes any soil constituent that neutralizes acid. Cu, Fe, Mn, and zinc (Zn) were extracted with diethyltriaminepentaacetic acid (Lindsay and Norwell 1978).

We applied additives to downy brome and *Hilaria* soils that manipulated availability of soil N, P, and K (Table 2). Because certain treatments could have unforeseen side effects or not fulfill intended goals, we used multiple ways to manipulate the availability of a given soil nutrient. Except for ferric oxide (Fe_2O_3) and zeolite (discussed below), all fertilizers were added at equivalent osmolar rates using Cannon et al. (1995) as a guide for additive levels. The concentrations we used (Table 2) resulted in the following osmotic potentials: 1 ×, 2 ×, 3 ×, 4 ×, and 5 × were the equivalent of − 0.46, − 0.91, − 1.37, − 1.83, and − 2.28 MPa, respectively. For Fe_2O_3 additions, we used levels similar to those of Solis and Torrent (1989), Carreira and Lajtha (1997), Hamad et al. (1992), and Samadi and Gilkes (1999).

To decrease available soil P, we added calcium oxide (CaO), Fe_2O_3, and calcium chloride ($CaCl_2$). CaO and Fe_2O_3 increase the buffering capacity of soil and can thus decrease available P (Hamad et al. 1992; Menon et al. 1990). $CaCl_2$ was used as a water-soluble alternative to CaO, as results from our initial experiments indicated CaO was difficult to dissolve. Also, Carreira and Lajtha (1997) found that addition of soluble $CaCl_2$ to a calcareous entisol resulted in less available P, presumably due to $CaCO_3$ precipitation induced by the added Ca. To increase available soil P, we added oxalic acid to free carbonate-bound P and sodium phosphate (Na_2HPO_4). To decrease available K, we used magnesium chloride ($MgCl_2$), MgO, and zeolite, a high cation-exchange capacity (≈220 $cmol_c\ kg^{-1}$), crystalline, hydrated aluminosilicate of volcanic origin (Ming and Mumpton 1989). The Mg compounds were intended to reduce plant-available K through competitive displacement of K from exchange sites (Haynes 1980; Thompson and Troeh 1978) and zeolite to adsorb exchangeable K (Ming and Mumpton 1989). Each treatment was added in aqueous solution to soil (except for zeolite, which is a solid) and stirred. Clinoptilolite[2] was charged with Na^+ by equilibration with 2-M NaCl for 5.5 d, during which the solution was replaced every 24 h. After drying, the zeolite was mixed in dry form with soil.

TABLE 2. Germination trial treatments. All concentrations except Fe_2O_3 and zeolite are ionically equivalent. The μmol_c value denotes the amount of positive or negative charge added by each compound, and the charge ratio is determined by dividing μmol_c value by 16.7, which is the amount of charge added by NaCl per gram of soil. These values are for the 1× treatment. Quantities were varied up to 5× the concentrations shown (10× in the case of zeolite).

Treatment	Additive	Amount added		Ratio of charge to NaCl charge	Water-solubility[a]
		mg g^{-1} soil	μmol_c g^{-1} soil		
− P	CaO	0.6	44.5	2.7	NWS
− P	$CaCl_2$	0.6	9.9	0.6	WS
− P	Fe_2O_3	28.6	1,074.5	64.5	NWS
+ P	Na_2HPO_4	1.6	22.2	1.3	WS
+ P	Oxalic acid	1.0	22.2	1.3	WS
− K	$MgCl_2$	1.1	22.2	1.3	WS
− K	MgO	0.7	33.3	2.0	NWS
− K	Zeolite	(10% by volume)			NWS
+ K	KCl	1.2	16.7	1.0	WS
+ P and K	K_2HPO_4	1.9	22.2	1.3	WS
+ K + N	KNO_3	1.7	16.7	1.0	WS
+ K + N	$KCl{\cdot}NH_4Cl$	0.6 KCl; 0.5 NH_4Cl	16.6	1.0	WS
+ K + P + N	$K_2HPO_4{\cdot}KNO_3$	1.0 K_2HPO_4; 0.8 KNO_3	19.4	1.2	WS
Osmotic control	NaCl	1.0	16.7		WS
Control	None				

[a] Abbreviations: WS, water-soluble; NWS, non-water-soluble.

We also amended *Stipa* soils, which do not support downy brome populations, to determine if nutrient additions could enhance downy brome germination and emergence. For N, P, and K additions, we first analyzed native soils (Table 1) and then added 1 ×, 2 ×, and 3 × those naturally-occurring levels using NH_4Cl, Na_2HPO_4, and KCl, respectively. Soil pH (1:1 slurry) was manipulated in + N and + P treatments with HCl. Because treatments added salts and thus observed effects could be attributable to osmotic stress, a sodium chloride (NaCl) treatment was used both as an indicator of osmotic stress and as an independent treatment.

Emergence trials were conducted from September 2000 to March 2001 and germination and emergence trials from January 2001 to March 2001. Six grams of the resultant mixture for each treatment was placed in 5 (first set of trials) to 10 (subsequent trials) petri dishes that were 3.7 cm in diameter. Trials were repeated five times; however, amendments that did not suppress downy brome emergence or did suppress *Hilaria* emergence in the first trials were dropped from subsequent trials. Only treatments that suppressed downy brome emergence were applied to *Hilaria* seeds, and *Hilaria* seeds were only tested in downy brome soils (presuming that restoration efforts would occur in invaded soils). Twenty seeds of *Hilaria* or downy brome were placed in each dish, pushed just under the soil surface, and allowed to incubate in a laboratory with fluorescent lighting (approximately 600 photons m^{-2} s^{-1}) and average minimum and maximum temperatures of 19 and 23 C, respectively. Trials ran 10 d; control seeds germinated in 3 to 5 d, and no additional germinations were noted after 7 d for any treatment. Deionized water was added to dishes when the soil was visually dry. Dishes were covered with plastic wrap overnight to prevent drying. Germination was recorded as radicle protrusion from the seed to at least 1 mm and emergence as coleoptile protrusion at least 2 mm above the soil surface. After each trial ended, seeds were exhumed to determine numbers of ungerminated seeds. Each dish was considered a replicate. The value reported for a given treatment is the grand mean of all dishes in all trials of that treatment.

Among untreated (control) soils, one-way analysis of variance (ANOVA) evaluated differences in arcsine-transformed downy brome germination and emergence data. Individual treatments were analyzed for differences from the control and among concentrations with ANOVA and post hoc Student–Newman–Keuls tests. For data presentation in the figures, we divided all data by the corresponding control values to standardize results specific to each trial. We also compared results from the NaCl treatments with other treatments as an indication of whether treatment effects were osmotic or ion-specific. For each concentration of each treatment, mean NaCl values were subtracted from the corresponding values of the treatment (except zeolite and Fe_2O_3, which were not added in ionically equivalent concentrations) and then compared with control values with a t test. Unless otherwise noted, statistical significance is reported when $P < 0.05$.

Results and Discussion

Chemical characteristics varied among the downy brome, *Hilaria*, and *Stipa* soils, most notably in NO_3, P, Ca, and Na, before we added amendments (Table 1). *Stipa* and *Hilaria* soils had much lower P, NO_3^-, and Ca than did the downy brome soil, whereas both *Hilaria* and downy brome soils had much higher K, Mg, and K–Mg than did *Stipa* soils. These differences in soil chemistry strongly affected the results of the experiments (see discussion below).

There were no significant differences in downy brome germination ($F = 0.4$, $P = 0.65$) or emergence ($F = 0.0$, $P = 1.00$) among the three unamended control (downy brome, *Stipa*, and *Hilaria*) soils. Downy brome germination in all three soils averaged a very high 99.7%, and emergence of all seeds averaged 92.5% in the downy brome and *Hilaria* soils. In contrast, germination and emergence of *Hilaria*

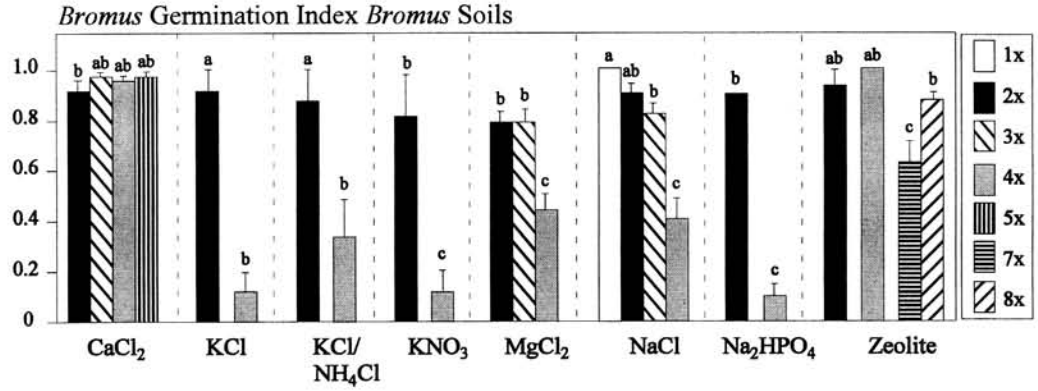

FIGURE 1. Mean ± SE number of downy brome seeds that germinated in downy brome soils. Values are standardized to the control (i.e., presented as a proportion of the control germination levels, with 100% of control = 1). Legend indicates multiples of concentrations of additives listed in Table 2. The letter "a" indicates no significant difference from the control. All other letters indicate significant ($P < 0.05$) differences from the control; different letters within a treatment indicate significant differences among concentrations. If error bars are lacking, germination was 100% for all replicates. Treatments with no significant differences from the control are not shown (CaO, Fe_2O_3, MgO).

seeds in the unamended downy brome soil averaged 68 and 66% respectively. However, 96.8% of the germinated *Hilaria* seeds emerged, indicating that germination and not emergence is a limiting step in *Hilaria* seedling establishment.

Additions to Invaded (Downy Brome–Dominated) or Invadable (*Hilaria*-Dominated) Soils

The first goal of these experiments was to find soil amendments that significantly reduced emergence without reducing germination (otherwise, germinable seeds may be released from inhibition once water-soluble ions flush out of the soil, e.g., with rainfall [Kurth et al. 1986; Manohar 1966]) in downy brome while not substantially affecting either process in *Hilaria*. Both non–water-soluble and water-soluble amendments were applied as treatments. The non–water-soluble treatments were added to reduce plant-available P (using CaO, Fe_2O_3, MgO) or K (using MgO, zeolite). In *Hilaria* soils, all four treatments reduced downy brome emergence without reducing germination (Figure 1; Table 3). In downy brome soils, only zeolite significantly reduced downy brome emergence (Table 3).

Many of the water-soluble treatments suppressed both germination and emergence in downy brome (Figure 1; Table 3). Whereas treatments that suppressed germination were eliminated from further consideration in this study, it is not known if germination was permanently or temporarily suppressed, and some of these treatments are still promising. Three treatments effectively suppressed downy brome emergence with only moderate effects on germination: $CaCl_2$, $MgCl_2$, and NaCl. Unlike the non–water-soluble treatments, they were equally effective on the two soil types.

The four treatments that were effective across the tested soils were then tested on *Hilaria* seeds (Figure 2; Table 3). Zeolite and $CaCl_2$ did not affect either germination or emergence of *Hilaria*. Whereas $MgCl_2$ and NaCl had some negative effect on *Hilaria*, this was substantially less than the effects on downy brome at any given concentration (Figure 2; Table 3). Our results also indicate that (1) soil levels of P and K are less critical for germination than emerging downy brome seedlings; (2) *Hilaria* is better able to tolerate low K and P availability than is downy brome; and (3) the effectiveness of additives will vary with antecedent soil chemistry.

These observed effects could have resulted from either ion-specific effects or osmotic stress, and distinguishing between these two effects is important in guiding future research efforts. Ion-specific effects appear actively involved because (1) ionically-equivalent applications of treatments did not always yield similar effects; (2) many treatments had significantly greater effects than did the NaCl treatment (Table 4); (3) the additives used are known to bind soil K and P. MgO binds P directly, and $MgCl_2$ added to calcareous soils forms $MgCO_3$, which binds P (Carreira and Lajtha 1997). Competitive displacement of K^+ by Mg^{2+} has been shown to reduce K^+ uptake by plants in several studies (Haynes and Goh 1978; Thompson and Troeh 1978); and (4) additions of both MgO and $MgCl_2$ have been previously observed to reduce downy brome germination (Howell 1998; Morrison 1999), emergence (Howell 1998; Miller 2000), and growth (Miller 2000).

Excessive osmotic stress could partially explain the observed effects. All treatments increased soil salt levels. For instance, the NaCl treatment at 1 × added 382 ppm Na^+, whereas natural soil levels at the study site are 40 to 96 ppm. A second indicator that osmotic stress was important was the fact that high levels of N, P, and K, generally expected to benefit the plant, decreased germination and emergence at higher concentrations. Multiple studies of various species have determined an inverse relationship between germination and osmotic stress (e.g., Susko et al. 1999; Wiggans and Gardner 1959). Goodwin et al. (1996) found that osmotic potentials down to − 1.0 MPa had little effect on downy brome germination, whereas Thill et al. (1979) showed downy brome germination and emergence decreasing with soil osmotic potentials at − 0.19 MPa. Our results show significantly diminished germination for most treatments with an osmotic potential of − 1.37 to − 1.83 MPa (i.e., at 3 to 4 × concentrations in Table 2) and emergence for most treatments at an osmotic potential of − 0.91 MPa (i.e., at 2 × the concentrations in Table 2; Figures 1–3).

Our results indicate that plant tissue emergence is more sensitive to salt concentrations than is the process of germination. In addition, *Hilaria* is clearly not as susceptible to the effect of high salt concentrations as is downy brome.

TABLE 3. Percent *Bromus* emergence in *Bromus* and *Hilaria* soils and *Hilaria* emergence in *Bromus* soils. Within a row, significant differences ($P < 0.05$) in *Bromus* emergence between *Bromus* and *Hilaria* soils are marked by an asterisk (*). Within a column (soil type) and within a treatment type, lowercase letters denote significant differences among different concentrations and the controls. The # symbol indicates significant suppression of emergence without significant suppression of germination. The ~ symbol indicates treatments that suppressed both germination and emergence.

		Bromus emergence (%)			*Hilaria* emergence (%)	
			Hilaria soils			
Treatment	Concentration	*Bromus* soils Mean	Mean	Significance	*Bromus* soils Mean	Suppression indicators
Control		100 a	100 a		66 a	
$CaCl_2$	2×	81 bc	65 b			
	4×	66 c	65 b		102 a	
	5×	46 c			88 a	#
CaO	2×	104 a	107 a			
	4×	103 a	20 b	*		
Fe_2O_3	4×	99 a	70 b	*		
KCl	2×	73 b	54 b			
	3×	11 c	35 b			# ~
	4×	2 c	30 b	*		# ~
$KCl{\cdot}NH_4Cl$	2×	78 b	80 b			
	3×	24 c	26 c			# ~
	4×	0 c	23 c			# ~
K_2HPO_4	2×	71 b	107 a	*		
	3×	9 c	76 a	*		
	4×	32 c	40 b			# ~
$K_2HPO_4{\cdot}KNO_3$	3×	13 b	59 b			
	4×	9 b	43 b			# ~
KNO_3	2×	73 b	76 b			
	3×	6 c	52 b			# ~
	4×	4 c	12 c			# ~
$MgCl_2$	2×	34 b	28 b		81 ab	
	3×	8 c	35 b	*	62 b	#
	4×	3 c	10 b	*	16 c	
MgO	4×	96 a	78 b			
NaCl	2×	61 b	52 b		97 a	
	3×	39 c	46 b		79 a	#
	4×	4 d	27 b	*	25 b	
Na_2HPO_4	2×	79 b	96 a			
	3×	11 c	41 b			# ~
	4×	0 c	16 b	*		# ~
Oxalic acid	4×	103 a	89 a			
Zeolite	2×	86 abc	87 b			
	4×	100 ab	52 b	*		
	6×	81 bcd				
	7×	56 c			101 a	#
	8×	65 c			112 a	#
	10×	15 d				#

It is possible that *Hilaria* seedlings can discriminate against Na^+ as an adaptation to growth in salty desert soils. A similar capability is found in tomato plants (*Lycopersicon esculentum* L.) (Kurth et al. 1986). Alternatively, it is perhaps not the discrimination against Na^+ uptake per se as much as preferential retention of other ions such as Ca^{2+} (Kurth et al. 1986) that ensures *Hilaria* success under stressful salt conditions.

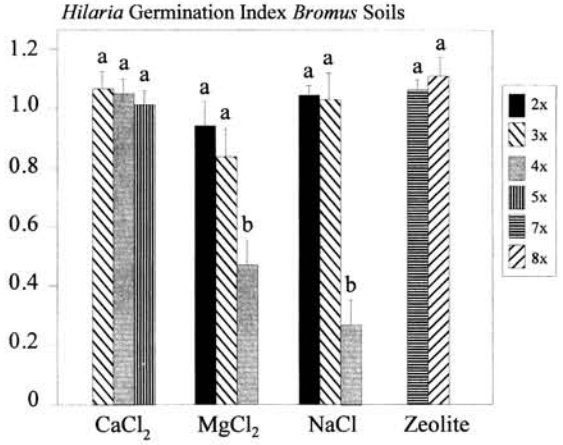

FIGURE 2. Mean ± SE number of *Hilaria* seeds that germinated, standardized to the control. See the caption of Figure 1 for explanation of significant differences. Treatments with no significant differences from the control are not shown (CaO, Fe_2O_3, MgO).

Additions to Noninvadable (*Stipa*) Soils

The second part of this experiment was to see the effects of "fertilizers" (N, P, K) in soils considered noninvadable (Belnap and Phillips 2001). Consequently, we added combinations of N, P, and K at 1 ×, 2 ×, and 3 × field levels to *Stipa* soils. Because germination in control soils was almost 100%, we were not able to assess any enhancement effects. Downy brome germination tended to be depressed at all levels of additional N and N + P + K, but this was only statistically significant at 3 × field levels (Figure 3). Emergence of the germinated seeds (proportional emergence) was generally not affected at 1 × or 2 × field levels but was depressed at 3 × field levels. Emergence was severely diminished at 8 × and 10 × field levels ($P < 0.01$; data not shown). The depression at the higher concentrations was expected as these compounds can be toxic at high concentrations (Haynes and Goh 1978). However, the depression at 3 × field levels was unexpected as N usually increases downy brome establishment and performance (Eckert and Evans 1963; Wilson et al. 1966). *Stipa* soils, which are not invadable by downy brome in the field (Belnap and Phillips 2001), have substantially greater $CaCO_3$ and lower P, Zn^{2+}, Cu^{2+}, Fe^{2+}, K^+, Mg^{2+}, Mn^{2+}, and NH_4^+ than do either *Hilaria* or downy brome soils (Table 1). We used NH_4^+, which, although providing an N supplement, can interfere with absorption of other ions such as K^+ (Haynes and Goh 1978; Thompson and Troeh 1978). However, adding KCl and $KCl{-}NH_4Cl$ yielded almost identical results and did not prevent depression of either germination or emergence. Addition of NH_4^+ and NO_3^- similarly suppressed both germination and emergence, supporting the idea that high levels of N alone are responsible for the observed depression.

Downy brome emergence was also diminished with increasing soil acidity in *Stipa* soils (Figure 4). Given the apparent susceptibility of downy brome to high salinity (or highly negative osmotic potential), the negative relationship between downy brome emergence and soil acidity may be accounted for by the greater solubilities of nutrients such as Ca^{2+}, Cu^{2+}, Fe^{2+}, K^+, Mn^{2+}, HPO_4^{2-}, and Zn^{2+} at low pH (Gadd 1999; Thompson and Troeh 1978). In contrast to our results, Egley and Duke (1985) state that weed germination should not be affected within the natural range of

TABLE 4. *t* Test values evaluating the differences between treatments and NaCl at corresponding concentrations. The (ND) denotes that a concentration of a treatment or the corresponding concentration of NaCl was not tested. Zeolite was not tested because its ionic additions to or subtractions from soil solution were not quantifiable. ***P < 0.001, **P < 0.01, *P < 0.05.

		Bromus soil				*Hilaria* soil
		Bromus seed		*Hilaria* seed		*Bromus* seed
Treatment	Concentration	Germination	Emergence	Germination	Emergence	Emergence
$CaCl_2$	2×	0.51	2.72	ND		0.71
	3×	9.14***	13.17***	0.58	5.50***	
	4×	29.32***	8.24***	16.45***	15.55***	3.58*
CaO	2×	—[a]	18.48***	ND	ND	26.23***
	4×	—[a]	37.83***	ND	ND	− 0.34
KCl	2×	0.24	0.64	ND	ND	0.63
	3×	ND	− 2.64	ND	ND	− 0.81
	4×	− 3.92*	− 0.57	ND	ND	0.35
$KCl{\cdot}NH_4Cl$	2×	− 0.17	1.54	ND	ND	2.15
	3×	ND	− 0.66	ND	ND	− 2.65
	4×	− 0.47	—[a]	ND	ND	− 0.42
K_2HPO_4	2×	ND	0.66	ND	ND	25.00***
	3×	ND	− 4.59*	ND	ND	1.59
	4×	ND	2.56	ND	ND	1.26
$K_2HPO_4{\cdot}KNO_3$	2×	ND	ND	ND	ND	5.42**
	3×	ND	− 2.51	ND	ND	0.67
	4×	ND	0.61	ND	ND	1.63
KNO_3	2×	− 0.52	0.54	ND	ND	1.19
	3×	ND	− 6.12**	ND	ND	0.42
	4×	− 3.60*	0.28	ND	ND	− 2.44*
$MgCl_2$	2×	− 3.03**	− 4.72***	− 1.21	− 1.79	− 2.14
	3×	− 0.55	− 15.21***	− 2.50*	− 2.02	− 1.51
	4×	0.69	− 0.26	2.31*	− 1.62	− 6.73***
MgO	2×	ND	ND	ND	ND	25.00***
	4×	ND	11.21***	ND	ND	6.19**
Na_2HPO_4	2×	− 0.01	1.47	ND	ND	4.13*
	3×	ND	− 2.05	ND	ND	− 0.22
	4×	− 6.88**	—[a]	ND	ND	− 1.59
Oxalic acid	2×	ND	ND	ND	ND	19.59***
	4×	ND	23.22***	ND	ND	4.51*

[a] SD = 0, and *t* test not performed.

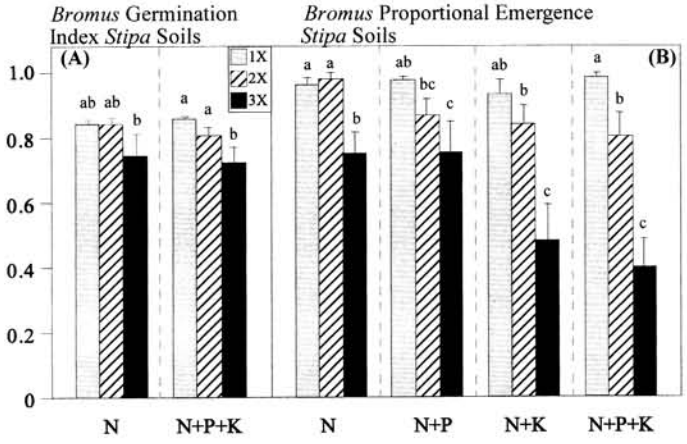

FIGURE 3. Mean ± SE downy brome (*Bromus tectorum* L.) (A) germination and (B) proportional emergence, standardized to control levels in *Stipa* soils. See the caption of Figure 1 caption for explanation of significant differences.

soil pH. We attempted to increase soil pH with NaOH and $CaCO_3$, but equilibration with atmospheric CO_2 or soil buffering prevented appreciable increases, and all buffer solutions investigated contained undesirable nutrients. In separate greenhouse studies we observed that downy brome germination at pH 9.9 was severely reduced, but this may have also been due to very high concentrations of Na^+ (data not shown). Decreased emergence was seen at all pH levels when high N (8.2 × field levels) was added, supporting the argument that high N concentrations reduce downy brome emergence.

Our results offer promising insight into control of downy brome populations in calcareous soils. One option for management of downy brome–invaded sites is to stimulate germination of downy brome seeds while inhibiting emergence. The dynamics of soil P and K appear to strongly affect downy brome performance as reducing the availability of K or P (or both) decreased downy brome emergence. *Hilaria*, on the other hand, appears much less sensitive to reductions in K and P availability in these soils. Of the tested amendments, $CaCl_2$ (at 4 × and 5 × field levels), $MgCl_2$ (at 3 × field levels), NaCl (at 3 × field levels), and zeolite (from 2

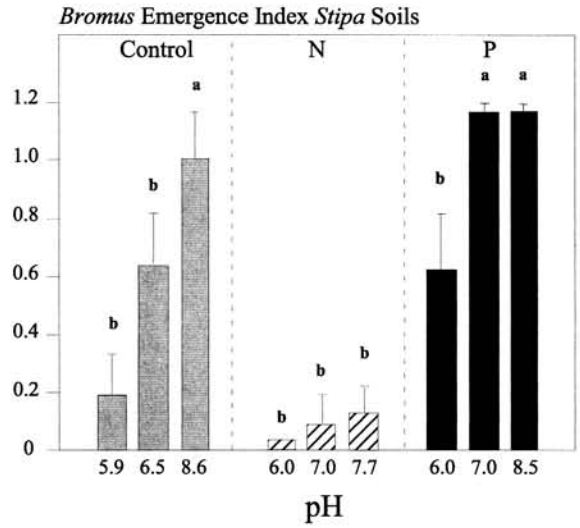

FIGURE 4. Mean ± SE downy brome (*Bromus tectorum* L.) emergence rates standardized to control levels in *Stipa* soils of varying acidity. Different superscripts indicate significant differences within a treatment. N levels were at 8.2 × and P at 2.3 × naturally occurring levels. Treatments with no significant differences from the control are not shown (germination: P, K, N + P, N + K, P + K; proportional emergence: P, K, P + K).

to 10 ×, depending on soil chemistry) have potential as management tools based on their ability to maximize downy brome germination and minimize downy brome emergence without negatively affecting *Hilaria* germination or emergence. In low-P soils, future studies should test CaO, Fe_2O_3, and MgO on downy brome. All these findings need field testing. Future studies should also determine whether *Hilaria* is representative of other native species in its response to these soil amendments.

Sources of Materials

[1] Southwest Seed, Inc., 13260 CR 29, Dolores, CO 81323.
[2] A form of zeolite, GSA Resources, Inc., P.O. Box 509, Tucson, AZ 85652.

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Salt-sensitivity of the exotic annual grass *Bromus tectorum L,* and facilitation of its growth by the native perennial grass *Hilaria jamesii*

Introduction

Bromus tectorum L. (hereafter referred to as *Bromus*) is a C_3 annual grass species that is also known as cheatgrass or downy brome (Mack 1981, Upadhyaya et al. 1986). The invasion of this species into western US ecosystems has had monumental consequences. *Bromus* has replaced native plant communities and the resultant changes in type and timing of food and cover have reduced native plant and animal diversity (Vail 1994). Greater wildfire frequency in cheatgrass habitat has further reduced native biodiversity and altered native vegetation structure (Whisenant 1990). The consequences of cheatgrass invasions are both of ecological and economic concern, given the deterioration of farm and rangeland habitat and the high cost of fire suppression (Mack 1981, Upadhyaya et al. 1986). In addition, *Bromus* alters soil food webs, biogeochemistry, and nutrient relations in ecosystems where it dominates (Belnap and Phillips 2001, Harper et al. 1996) in a way that reinforces its own presence (Woodward et al. 1984, Harper et al. 1996, Belnap and Phillips 2001).

Southern Utah grasslands have experienced a substantial invasion by *Bromus*. Native grass communities once dominated by *Hilaria jamesii* (a rhizomatous C_4 perennial, hereafter referred to as *Hilaria*) are particularly susceptible to invasion, whereas those dominated by *Stipa comata* and *S. hymenoides* (hereafter referred to as *Stipa*) exhibit little, if any, invasion (Belnap and Phillips 2001). Soils where *Bromus* and *Hilaria* occur have higher silt, potassium (K^+), and K^+/magnesium (Mg) ratio compared to soils dominated by *Stipa* (Kleiner & Harper 1972, 1977a; Miller 2000; Belnap and Phillips 2001). Previous studies show K^+ additions to soils can stimulate *Bromus* growth (Howell 1998, Morrison 1999). Miller (2000) showed *Bromus* emergence is inhibited when exchangeable Mg^{2+} is added to soils, which may block K^+ uptake (Haynes & Goh 1978, Thompson & Troeh 1978, Haynes 1980). This suggests *Bromus* is limited by water and K^+. *Bromus* growth is also positively associated with bioavailable phosphorus and negatively associated with soil acid neutralizing potential (ANP; this is the acid-buffering capacity of the soil to due to carbonates and reactive oxides such as magnesium [Mg^{2+}], zinc [Zn^{2+}], manganese [Mn^{2+}], and iron [Fe^{2+}]), suggesting *Bromus* is also limited by soil levels of plant-available P (Eckert & Evans 1963, Miller 2000).

Restoring *Bromus* infested ecosystems is a high priority for many land managers. However, seeding natives into established *Bromus* stands often fails, and this failure has been attributed to competition from *Bromus*. Therefore, we tested different soil amendments intended to negatively affect the growth of *Bromus* but not *Hilaria*. Based on previous studies, our treatments focused on altering soil levels of P and K^+. Our predictions were that (1) decreasing K^+ availability would inhibit *Bromus* growth, whereas adding K^+ would increase growth and (2) *Bromus* would respond positively to P additions and negatively to the addition of compounds that bind P. We also expected all these treatments to affect *Hilaria* less than *Bromus*, given that *Hilaria* is a native perennial adapted to growing in fluctuating and low nutrient environments.

Methods

Sandy loam soils of the Begay series were collected from Canyonlands National Park (CNP), a cold semiarid ecosystem in southeastern Utah (~1500 m above sea level, average

annual precipitation and temperature, 214 mm and 11.6ºC, respectively; Miller 2000) in December 1999. Soils were sieved (2 mm sieves) and sent to the Brigham Young University Soil and Plant Analysis Lab for analysis. Phosphorus and available K^+ were extracted with $NaHCO_3$ (Olsen et al. 1954 and Schoenau et al. 1993, respectively). Exchangeable cations were extracted with ammonium acetate ($NH_4C_2H_3O_2$; Thomas 1982). Organic matter (OM) was determined by the Walkley-Black (1934) procedure, and electrical conductivity (EC) and pH with a saturated paste (Rhoades 1982). Texture was determined by the hydrometer method, CEC by sodium saturation (Chapman 1965), total N by Kjeldahl analysis (Bremner 1996), and ANP by HCl neutralization (Allison & Moodie 1965). Roots from ten plants each of *Bromus*, *Stipa*, and *Hilaria* were also collected in the field and analyzed for cation exchange capacity (CEC). Leaves from *Bromus* and *Stipa* growing alone and together in the field were also collected and analyzed for carbon isotopes at the University of Utah's Stable Isotope Facility.

In February 2000, each of 270 (4 cm x 16.8 cm) fiberglass pots were filled with 161 g of the CNP soil. Nine soil amendments were added at equivalent osmolar rates and at concentrations similar to Cannon et al. (1995; Table 1) except for zeolite (see below). Because some treatments could have unforeseen side effects or not fulfill the intended goal, we used multiple ways of altering plant-available soil nutrients. To increase plant-available P, we added Na_2HPO_4 and oxalic acid. Oxalic acid is an organic acid produced by plant roots, mycorrhizae, and other organisms (Allen et al. 1996) that can solubilize or compete for exchange sites with soil Ca^{2+}, Fe^{2+}, K^+, Mg^{2+}, and P, keeping these elements available to local biota (Staunton & LePrince 1996). To decrease plant-available P, we used CaO to increase soil ANP and thus the capacity of biogenic acids to solubilize P. To increase K^+, we used KCl and K_2HPO_4. To decrease K^+, we used zeolite and $MgCl_2$. Zeolite is a high-CEC (220 $cmol_c\ kg^{-1}$), crystalline,

Additive	**Intended effect**	**Amount added mg g^{-1}soil**
Na_2HPO_4	+ phosphorus (P)	1.58
CaO	- P via increased acid neutralizing potential	0.62
KCl	+ K	1.24
Zeolite	- K	(10% by volume)
$MgCl_2$	- K	1.06
K_2HPO_4	+ P and K	1.93
Oxalic acid	- acid neutralizing potential	1.00
(nothing)	Control	

Table 1 Ammendments added, intended effect, and the amount of each amendment added.

hydrated aluminosilicate of volcanic origin that can preferentially bind K^+ (Ming & Mumpton 1989). The presence of $MgCl_2$ can reduce K^+ through competitive displacement of K^+ from root exchange sites by Mg^{2+} (Haynes & Goh 1978, Thompson & Troeh 1978, Haynes 1980). When $MgCl_2$ is added to calcareous soils, it can also form $MgCO_3$, which binds P in a plant-unavailable form. Except zeolite, each treatment was added in aqueous solution to 30 of the pots. Clinoptilolite (a form of zeolite, GSA Resources, Inc., Tucson, AZ) was charged with Na^+ by equilibration with 2M NaCl for 5.5 days; solution was changed out every 24 h. It was then mixed with soil in a larger container and added to the pots.

Bromus seeds were collected from the Canyonlands Needles district and were fully after-ripened. *Hilaria* seeds were purchased from Southwest Seed (in nearby Cortez, CO). In early March 2000, either ten *Hilaria* or ten *Bromus* seeds were planted in ten pots of each soil treatment ("monoculture" pots). In the remaining ten pots of each treatment, five *Hilaria* and five *Bromus* seeds were planted together ("combination" pots). Pots were placed in the greenhouse at Denver University.

Three weeks after planting, plants were thinned to two *Bromus* individuals and five of the smaller, slower-growing *Hilaria* individuals. Plants were harvested while root biomass was small relative to the soil volume to avoid nutrient competition. All pots and temperatures were monitored daily in the greenhouse and received de-ionized water when the surface soil was dry. Temperature minima and maxima averaged 17 and 27 C, respectively, during growth. Tissue from the monoculture pots was harvested, ground, and analyzed for nutrients. Nitrogen was run on a CHN Autoanalyzer and other elements were digested in perchloric acid and measured with inductively-coupled plasma spectrometry**.** There was insufficient *Hilaria* tissue for analysis of the K_2HPO_4 treatment or of *Bromus* tissue for analysis of the Na_2HPO_4 treatment or N in the control treatment. Roots biomass was analyzed for a subset of treatments in the monoculture pots. After above-ground parts were harvested, all roots were gently separated from the soil, dried, and weighed.

Analysis of the biomass data required transformations to meet normality assumptions, for which we took the square root of average *Bromus* biomass and the 4^{th}-root of average *Hilaria* biomass. All data was analyzed using ANOVA to distinguish differences among treatment effects. T-tests were used to analyze biomass between monoculture and combination pots within the same treatment. All statistics were analyzed using SPSS Release 12.

Results

Texture and chemistry of the collected soils are presented in Table 2. The average biomass of *Hilaria* and *Bromus,* grown alone and together are presented in Figure 1. When *Hilaria* was grown alone, no treatment resulted in a decline in biomass. However, one of the eight treatments (K_2HPO_4) showed a stimulation of *Hilaria* growth, and zeolite showed an almost significant tendency to stimulate growth as well. When *Hilaria* was grown with *Bromus*, there again was no effect of any treatments except Na_2HPO_4 which stimulated growth and zeolite which tended to stimulate growth. The presence of *Bromus* had a striking effect on *Hilaria* growth, reducing it by about 50% in most treatments compared to the monoculture pots ($p < 0.01$) with the exception of the Na_2HPO_4 treatment.

In contrast to *Hilaria*, *Bromus* biomass when grown in monoculture was significantly reduced by all treatments except CaO. This was surprising, as some of the treatments (e.g., KCl, K_2HPO_4, Na_2HPO_4, oxalic acid) were intended to stimulate *Bromus* biomass. However, when

	Bromus soils
P (ppm)	17
Available K^+ (ppm)	198
Exchangeable Ca^{2+} (ppm)	2568
Exchangeable K^+ (ppm)	295
Exchangeable Mg^{2+} (ppm)	129
Exchangeable K^+/Mg^{2+}	2.2
Exchangeable Na^+ (ppm)	40
OM (%)	0.4
EC (dS/M)	1.1
pH	7.8
% Sand	72
% Silt	14
% Clay	14
Total N (ppm)	74
NH_4-N (ppm)	7.4
NO_3-N (ppm)	20
$CaCO_3$ (%)	3.2
Cu^{2+} (ppm)	0.6
Fe^{2+} (ppm)	3.7
Mn^{2+} (ppm)	4.6
Zn^{2+} (ppm)	0.3

Table 2. Characteristics of soils from the *Bromus* dominated site

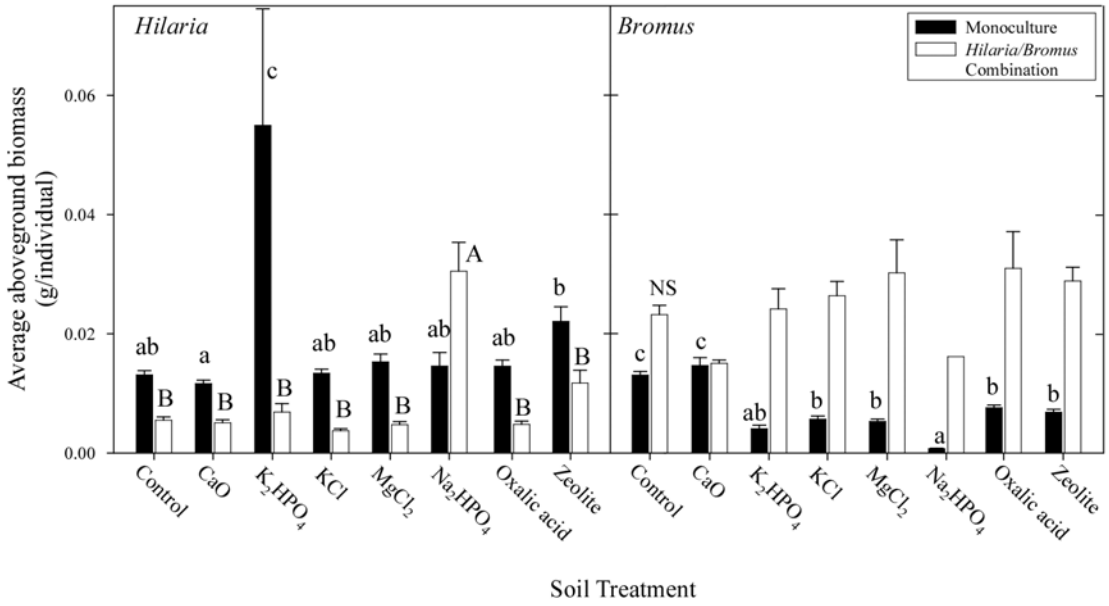

Figure 1. Above ground biomass of *Hilaria* and *Bromus* individual in monoculture and combination pots. Small roman letter indicate significant differences among the monoculture pots; capital roman letters indicate significant differences among the combination pots. (There was no significant differences in *Bromus* biomass among the combination pots.) All comparisons between the monoculture and combination pots within a plant type were significantly different (p <0.05).

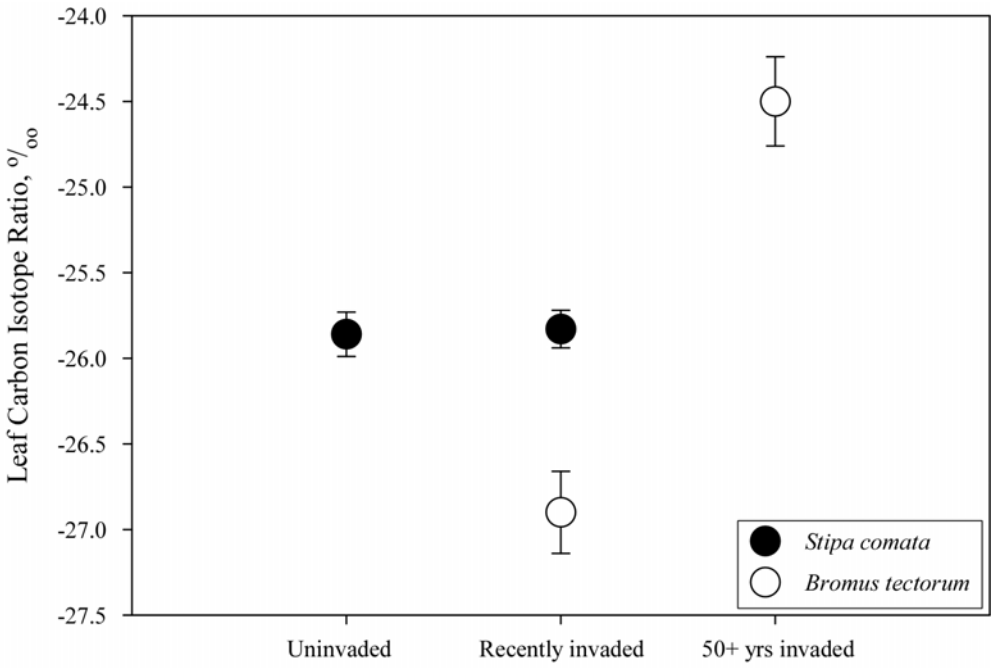

Figure 2. Leaf tissue carbon isotope ratios from sites where *Hilaria* plants were growing among other *Hilaria* plants (not invaded), from sites where *Bromus* and *Hilaria* were growing intermixed (recent invasion) and sites where *Bromus* plants were growing among other *Bromus* plants (historic invasion). Isotopic ratios of *Stipa* leaves were not significantly different between sites, whereas *Bromus* isotopic ratios were significantly different among sites (p<0.001).

		Treatment								
		Control	CaO	KCl	K_2HPO_4	$MgCl_2$	Na_2HPO_4	Oxalic acid	zeolite	Control B/H
Hilaria	Ca^{2+}	0.89^{b}	0.74^{b}	1.07^{a}		0.85^{b}	0.25^{d}	0.78^{b}	0.29^{d}	1.46
	Cu^{2+}	0.001	0.001	0.001		0.001	0.001	0.002	0.0009	2.7
	Fe^{2+}	0.012^{b}	0.025^{ab}	0.032^{a}		0.024^{ab}	0.019^{ab}	0.025^{ab}	0.014^{b}	1.92
	K^{+}	2.60^{a}	2.13^{ab}	2.64^{a}		1.79^{b}	2.09^{ab}	2.20^{ab}	1.79^{b}	2.21
	Mg^{2+}	0.30^{b}	0.21^{c}	0.24^{c}		0.51^{a}	0.20^{c}	0.25^{c}	0.20^{c}	1.63
	Mn^{2+}	0.015^{ab}	0.013^{b}	0.019^{a}		0.016^{ab}	0.013^{b}	0.011^{b}	0.016^{ab}	0.87
	N	2.38^{a}	1.66^{b}	1.78^{ab}	1.960^{ab}	1.78^{b}	1.37^{b}	1.23^{b}	1.48^{b}	
	Na^{+}	0.005^{c}	0.003^{c}	0.004^{c}		0.003^{c}	0.037^{a}	0.004^{c}	0.023^{b}	0.48
	P	0.15^{b}	0.11^{b}	0.09^{b}		0.10^{b}	0.43^{a}	0.14^{b}	0.15^{b}	2.00
	S	0.23	0.23	0.28		0.24	0.17	0.19	0.19	1.13
	Zn^{2+}	0.003	0.003	0.006		0.005	0.003	0.004	0.003	1.67
	K/Ca	2.9	2.9	2.5		2.1	8.5	2.8	6.3	1.51
	K/Mg	8.6	10.1	11.2		3.5	10.7	8.8	9.2	1.35
	K/Na	518	707	660		597	56	548	78	4.61
	K/P	18	20	31		19	5	16	12	1.11
	K/N	1.1	1.3	1.5		1.0	1.5	1.8	1.2	
	P/Ca	0.2	0.1	0.1		0.1	1.7	0.2	0.5	1.37
	P/Mg	0.5	0.5	0.4		0.2	2.2	0.5	0.7	1.22
	P/Na	29	35	21		32	11	34	6	
	P/N	0.1	0.1	0.0		0.1	0.3	0.1	0.1	
	Ca/Na	178	247	267		283	7	194	12	

		Treatment							
		Control	CaO	KCl	K_2HPO_4	$MgCl_2$	Na_2HPO_4	Oxalic acid	zeolite
Bromus	Ca^{2+}	1.31^{c}	1.38^{b}	1.27^{d}	0.67^{f}	1.36^{b}		1.58^{a}	0.96^{e}
	Cu^{2+}	0.003^{cd}	0.002^{d}	0.003^{bc}	0.003^{bc}	0.003^{bc}		0.005^{a}	0.002^{cd}
	Fe^{2+}	0.023	0.039	0.035	0.032	0.037		0.037	0.044
	K^{+}	5.7	5.8	6.7	7.0	5.1		5.9	5.8
	Mg^{2+}	0.49^{b}	0.41^{d}	0.39^{cd}	0.32^{e}	1.04^{a}		0.47^{bc}	0.47^{bcd}
	Mn^{2+}	0.013	0.011	0.019	0.013	0.016		0.023	0.017
	N		2.73^{c}	3.30^{ab}	2.71^{bc}	3.44^{ab}	3.44^{b}	2.41^{c}	2.40^{c}
	Na^{+}	0.002^{e}	0.002^{f}	0.004^{d}	0.005^{c}	0.003^{d}		0.006^{c}	0.063^{a}
	P	0.29^{c}	0.20^{d}	0.03^{c}	1.01^{a}	0.30^{c}		0.51^{b}	0.50^{b}
	S	0.26	0.29	0.26	0.24	0.23		0.30	0.35
	Zn^{2+}	0.005^{c}	0.005^{c}	0.007^{b}	0.005^{c}	0.005^{c}		0.009^{a}	0.007^{b}
	K/Ca	4.4	4.3	5.3	10.5	3.7		3.7	6.0
	K/Mg	12	14	17	22	5		13	12
	K/Na	2388	3644	1718	1300	1539		1021	91
	K/P	20	30	23	7	17		12	12
	P/Ca	0.2	0.1	0.2	1.5	0.2		0.3	0.5
	P/Mg	0.6	0.5	0.7	3.2	0.3		1.1	1.1
	P/Na	121	122	74	187	91		88	8
	Ca/Na	541	856	325	124	412		272	15

Table 3. Mean percentage of aboveground tissue nutrient contents. All biomass is from monocultures. Different subscripts within a nutrient indicate significant (p<0.05) difference among treatments along a row. Missing data indicate that there was insufficient sample

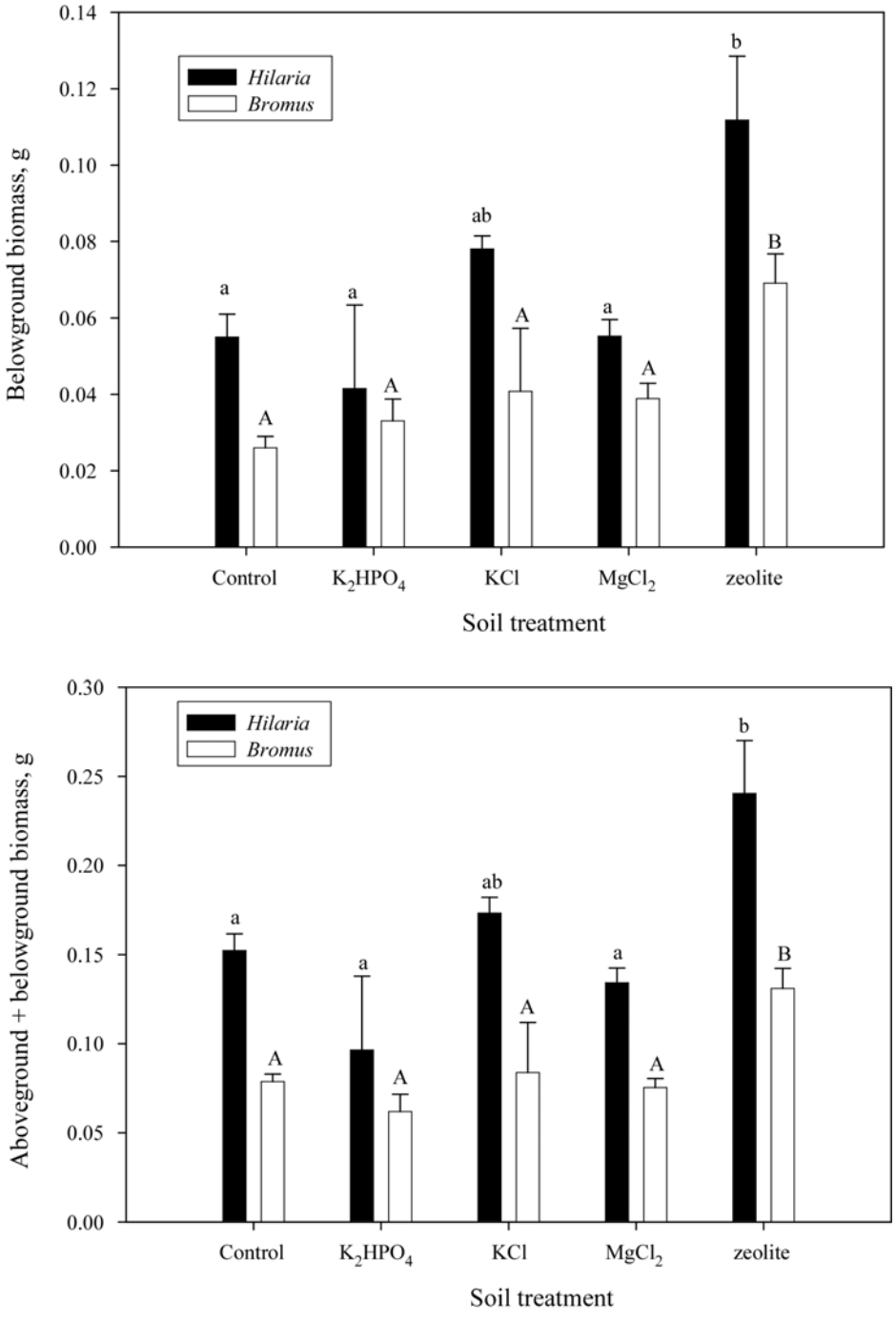

Figure 3. Below-ground biomass and total biomass (above-ground + below-ground biomass) of *Hilaria* and *Bromus* roots in selected treatments. Small roman letters indicate significant differences among *Hilaria* pots. Large roman letters indicate significant differences among *Bromus* pots.

Bromus was grown with *Hilaria*, the treatments no longer had a negative effect. In addition, *Bromus* biomass increased up to 400% relative to the monoculture pots. This facilitation of *Bromus* by the presence of a native plant was also seen in the field: the carbon isotopic ratio of *Bromus* growing alone was much less negative than the isotopic ratio of *Bromus* growing next to the native grass *Stipa*, whereas there no significant change in *Stipa* growing alone relative to *Stipa* growing with *Bromus* (Figure 2).

As would be expected when comparing an annual with a perennial plant, we found that the annual *Bromus* roots had a much higher CEC (CEC = 11.5 meq/100 g root, S.E. 1.9) than the native perennial roots of *Hilaria* **(**CEC **=** 5.1 meq/100 g root, S.E. 0.5) or *Stipa* (CEC = 1.2 meq/100 g root, S.E. 0.3). In addition, as expected due to life form and root CEC differences, *Bromus* leaves in almost all the treatments had higher elemental concentrations than the *Hilaria* tissue (Table 3). Although N was not analyzed in control *Bromus* tissue, *Bromus* N levels were 2-3 times that of *Hilaria* N levels in all treatments, indicating that N was probably also higher in *Bromus* controls than *Hilaria*. However, sodiumwas higher in tissues of *Hilaria* than *Bromus* in most treatments. The treatments where this was not true were the treatments where Na^+ was added (Na_2PO_4, zeolite); here, tissue levels of *Hilaria* were higher. In these treatments, *Bromus* had much higher levels of Na^+ than *Hilaria*. *Bromus* tissue also had consistently high levels of K^+ among all treatments, indicating this species likely has higher requirements for this cation (Tilman 1982). In addition, *Bromus* may utilize K^+ to avoid Na^+ stress when Na^+ levels are high in the soil, as seen in other plant species (e.g., Kaya et al. 2002, Maser et al. 2002, Golldack et al. 2003, Zeng et al. 2003). However, K^+ levels in *Bromus* stayed fairly constant, regardless of tissue Na^+ levels, which may indicate that *Bromus* has a limit to how much K^+ can be used for this purpose. *Bromus* and *Hilaria* roots responded in a similar fashion in the subset of treatments examined **(**control, KCl, $MgCl_2$, K_2HPO_4, and zeolite, monoculture pots only; Figure 3). For both species, root biomass was greatest in zeolite treatment and not different among the other treatments. However, this pattern was not reflected in above-ground biomass, as no treatment reduced *Hilaria* biomass in the monoculture pots. In addition, whereas *Hilaria* biomass was high in the zeolite treatment, *Bromus* biomass was very low. The K_2HPO_4 treatment had the greatest aboveground *Hilaria* biomass, but the smallest amount of root biomass.

Discussion

Treatment Effects

Na_2HPO_4: The addition of Na_2HPO_4 to the *Hilaria-Bromus* combination pots resulted in a dramatic increase in *Hilaria* biomass, yet adding this same amendment to the *Bromus* or *Hilaria* monoculture pots resulted in either a dramatic lowering of biomass (*Bromus*) or no effect (*Hilaria*). The Na_2HPO_4 treatment was intended to increase available soil P. However, the Na_2HPO_4 treatment also added 512 ppm Na^+, a nonessential element to C_3 species such as *Bromus* (Thompson & Troeh 1978, Marschner 1985). All additives except zeolite, which is osmotically inert, were added at equivalent osmolar concentrations; therefore, the effects of Na_2HPO_4, therefore, cannot be attributed to osmotic effects alone, or a similar response would have been seen in the other treatments. *Bromus* may have been directly inhibited by this large Na^+ addition. Na_2HPO_4 also increased soil pH from 8.5 to 9.9, a pH at which multiple elements are rendered unavailable (Thompson & Troeh 1978). And lastly, cation uptake may have been inhibited through ionic competition with Na^+ at root exchange sites. Indeed, *Hilaria* tissue nutrient analysis shows a reduction in uptake of Ca^{2+}, K^+, Mg^{2+}, Mn^{2+}, N, and S in the Na_2HPO_4

treatment relative to the control in the monoculture pots (Table 3). Unfortunately, there was not sufficient tissue to analyze *Bromus* for this treatment to see if it responded in a similar manner. *Hilaria* biomass clearly benefitted from the Na_2HPO_4 treatment in combination pots, where the highest levels of salt were added. This suggests *Hilaria* not only tolerates high soil Na^+ but may belong to a group of C_4 grasses that manifests supplementary growth in response to additional Na^+ (Marschner 1985). It is not clear, however, why *Hilaria* did not respond similarly in the combination compared to the monoculture pots: perhaps Na^+ was only beneficial to *Hilaria* in the presence of *Bromus* competition for other nutrients such as K^+.

K_2HPO_4 and KCl: Previous studies in this region have indicated that *Bromus* may be K^+ limited (Belnap and Phillips 2001, Morrison 1999, Howell 1998, Belnap in prep). Based on these previous studies, we did not expect the observed negative response of *Bromus* biomass to the K_2HPO_4 and KCl treatments. Whereas the K^+ concentrations in *Bromus* tissue indicate more K^+ was indeed made available and utilized by *Bromus* in this treatment, the negative biomass response may have been attributable to ionic competition for root exchange sites between K^+ and the other essential elements Ca^{2+}, Mg^{2+}, Na^+, and/or NH_4^+ (Epstein 1972, Haynes & Goh 1978, Thompson & Troeh 1978, Haynes 1980, Jeffrey 1987, Barber 1995). The suppression of Ca^{2+} and Mg^{2+} uptake is also supported by the tissue concentration data. In addition, these treatments resulted in significantly higher concentrations of tissue Na^+, despite conventional claims that K^+ easily outcompetes Na^+ in root uptake experiments (when Na^+ concentrations don't overwhelm those of K^+; Epstein 1972, Jeffrey 1987). This may be due to K^+ replacing Na^+ from soil exchange sites (Thompson & Troeh 1978), resulting in more Na^+ in a plant-available form. Lastly, *Bromus* may have reacted negatively simply to the additional salts in the soils the treatments added.

Hilaria did not respond to either K_2HPO_4 or KCl in the combination pots. In contrast, *Hilaria* in monoculture showed a dramatic surge of growth with the K_2HPO_4 addition. Because increased growth was seen in *Hilaria* in combination pots with the Na_2HPO_4 addition as well, it appears *Hilaria* was responding to not to the addition of K^+ but that of P, with no negative Na^+ effect. Or, as conjectured above, perhaps Na^+ is beneficial to *Hilaria* in the presence of *Bromus* competition for K^+. Tissue P concentrations in *Hilaria* under the Na_2HPO_4 support this hypothesis (there was insufficient *Bromus* tissue from the K_2HPO_4 treatment for analysis). In addition, native species' response to K^+ fertilizer typically are rare (Thompson & Troeh 1978, Havlin & Westfall 1985, Miller 2000). However, there is a caveat to our interpretation, as the increase in *Hilaria* biomass with Na_2HPO_4 was only seen in monoculture pots and the increase with K_2HPO_4 was seen only in the combination pots, indicating other factors associated with *Bromus* likely modulated this response.

$MgCl_2$ and zeolite: As mentioned above, *Bromus* growth has been shown to be positively associated with soil K^+. $MgCl_2$ was added to reduce plant-available K^+ via competitive displacement of K^+ from root exchange sites by Mg (Haynes & Goh 1978, Thompson & Troeh 1978, Haynes 1980). Tissue K^+ concentrations in this experiment indicate that as intended, $MgCl_2$ appeared to reduce uptake of K^+ in *Bromus*. Again, as expected, *Bromus* growth was reduced in the monocultures. However, as noted above, direct addition of K^+ did not stimulate *Bromus* growth, so it is not clear that the displacement of K^+ by Mg was the reason for the reduction in *Bromus* biomass.

Zeolite was also added to reduce plant-available K^+, as it can preferentially bind this nutrient, and was shown to be effective in a previous study (Belnap et al. 200xxsherrod germ).

However, K^+ tissue concentrations with the zeolite treatment actually increased in *Bromus* and did not change in *Hilaria*, indicating this treatment did not work for this purpose. However, zeolite did add tremendous amounts of Na^+ to the soil, and we attribute the observed decline in *Bromus* biomass in this treatment to a salt suppression effect. *Hilaria* again was not affected by the additional Na^+; in fact, it tended to stimulate biomass in the monoculture pots.

Oxalic acid: *Bromus* showed a large increase in tissue concentrations of P when oxalic acid was added to the soil, as expected. There was also a large increase in many other nutrients, including Ca^{2+}, Cu^{2+}, Mg^{2+}, Mn^{2+}, Na^+, and Zn^{2+}, likely attributable to the ability of oxalic acid to solubilize soil nutrients (Allen et al. 1996) and/or to compete for soil exchange sites (Staunton & LePrince 1996). This argues strongly for a luxury uptake phenomenon on the part of *Bromus*, even when detrimental to the plant (e.g., Na^+ in the Na_2HPO_4 and zeolite treatments), and is likely facilitated by *Bromus*' high root CEC.

CaO: The CaO treatment was intended to decrease levels of plant-available soil P and levels of P in *Bromus* tissue indicates that this treatment was successful. However, we did not see the expected decline in *Bromus* biomass. There are several possibilities to explain this. First, CaO was very difficult to dissolve, and much of it was not incorporated into the soil. Secondly, it may be that the decline in P was offset by attendant increases in other nutrients (Ca^{2+}, K^+, Fe^{2+}, and S). Thirdly, the reduction of tissue Na^+ may have been beneficial. This is may be another indication that *Bromus* is salt-sensitive, as tissue Na^+ did not increase in this treatment and *Bromus* biomass did not decline. And lastly, the lack of response supports the idea that the adverse affects noted with the other amendments were due to osmotic effects reducing water availability.

Non-target nutrients: There were some interesting patterns among elements not targeted by specific treatment additions. In both *Bromus* and *Hilaria* tissues, Fe^{2+} concentrations increased in all treatments (although this increase was not always statistically significant). In *Hilaria*, tissue concentrations of Ca^{2+} declined with the addition of Na^+, while tissue Na^+ increased with the addition of K^+. Mg^{2+} declined in all treatments except where it was directly added ($MgCl_2$). *Hilaria* tissue N declined in all treatments. In contrast to *Hilaria*, Ca^{2+} in *Bromus* tissue did not respond to Na additions, and was negatively affected with K^+ additions. Mg concentrations in *Bromus* appeared less sensitive than those in *Hilaria*, as only a few treatments showed a decline in this nutrient. In *Bromus* tissue, concentrations of Cu^{2+}, Zn^{2+}, and Mn^{2+} appeared elevated in many treatments, although lack of replication precluded statistical comparisons in some cases.

Salt-sensitivity of *Bromus*: As can be seen in Figure 1, six of our seven amendments had a negative effect on *Bromus* in monoculture pots. This result was a surprise, as three of the treatments that resulted in a *Bromus* decline were expected to have a positive effect via the addition of K^+ and P. This alerted us to the possibility that *Bromus* may be sensitive to soil salt levels, regardless of the type of salt present. When looking at all the treatments together, the treatments in which *Bromus* biomass declined were those that showed an increase in tissue concentrations of Na^+. The presence of *Hilaria* may have ameliorated the impact of soil salts on *Bromus*, as *Hilaria* uptake of these salts would reduce ambient levels, perhaps making the soil environment more tolerable for *Bromus*.

We have observed a similar negative response of *Bromus* to high salt levels in previous field and laboratory studies. When we applied N, P, and K^+ to field plots with the intention to increase germination, emergence, and biomass, we instead saw large reductions in all three

processes (Belnap et al., in prep). In a previous laboratory study of *Bromus* and *Hilaria*, germination and emergence was reduced in *Bromus*, but not *Hilaria*, at increased soil salt levels, regardless of the type of salt added (Belnap et al. 2003). And finally, a recent laboratory study examining the impact of NaCl on *Bromus* and *Hilaria* germination again showed *Bromus* was much more sensitive to salt than *Hilaria* (Newingham and Belnap, in prep.).

Bromus may be less able than *Hilaria* to restrict cation uptake when soil levels are high. This may be due to *Bromus* having a much higher root CEC than *Hilaria*. Coulomb's law predicts that *Bromus*, with the more highly charged root, would attract charged particles more strongly than the less-charged *Hilaria* roots. That said, *Bromus* does appear able to reduce uptake of Na^+ by substituting Ca^{2+} and/or K^+, as *Bromus* leaves often had only half the Na^+ levels of *Hilaria* leaves, while having much higher levels of Ca^{2+} and K^+. The ability of *Bromus* to discriminate against Na^+ much more effectively than the native grass *Stipa* was also recently seen in a recent field trial at our site (Miller et al. in prep). Lastly, *Bromus* may be more sensitive than *Hilaria* to the reduction of water availability when osmotic potentials are increased.

Facilitation of Bromus *by* Hilaria

When grown together, *Bromus* and *Hilaria* both had very different responses to our amendments than when grown apart in monoculture pots. *Bromus* biomass increased dramatically with the presence of *Hilaria*, whereas *Hilaria* biomass decreased in the presence of *Bromus*. In addition, the field measures of the carbon isotopic ratios verified that the presence of a native grass enhanced *Bromus* performance.

There are multiple scenarios that could explain the decline of *Hilaria* and the observed facilitation of *Bromus* in the combination pots. These include: 1) *Hilaria* uptake of Na^+ and other cations reduced salt stress on *Bromus*; 2) *Bromus* tapped into *Hilaria's* mycorrhizal network, thus gaining access to water and nutrients that *Hilaria* would have otherwise received; 3) *Hilaria* declined because *Bromus* outcompeted it for soil water and nutrients found in the bulk soil; and/or 4) *Hilaria* declined because *Bromus* outcompeted *Hilaria* for nutrients and/or water exuded by *Hilaria* via hydraulic redistribution.

Scenario 1, Cation removal: Tissue concentration data shows that *Hilaria* did take up substantial amounts of Na^+ and other cations, especially in treatments where a specific cation was high (e.g., for Na^+, the treatments Na_2HPO_4 and zeolite). Thus, removal of cations by *Hilaria* may partially explain improved *Bromus* performance in these treatments. However, for Na^+ specifically, the amount removed by *Hilaria* in treatments that did not add Na^+ was low and unlikely to explain the observed increase in *Bromus* performance. In addition, this scenario does not specifically address why *Hilaria* performance would be reduced when *Bromus* was present.

Scenario 2, Mycorrhizae: There is ample evidence that plants can tap into other species' mycorrhizal networks (Callaway, et al. 2001) and "steal" nutrients and water. Although no study has addressed this possibility for *Bromus* and *Hilaria*, it is a highly viable hypotheses and should be investigated further.

Scenario 3, Competition for water and nutrients: Similar to our observations, Harris (1967) found that when *Bromus* and *Agropyron spicatum* were grown in common pots, the dry weight of *Agropyron* decreased while the root growth of *Bromus* increased. This was attributed to *Bromus* roots depleting soil moisture before the root systems of *A. spicatum* could effectively utilize it. Because water was not limiting in our greenhouse studies, and given the much higher root CEC of *Bromus*, we suggest that *Bromus* may have also been able to outcompete *Agropyron*

for soil nutrients. (Scenario 4 below offers another explanation of Harris' findings.) The idea that *Bromus* is able to outcompete native species for nutrients is supported by our observations, as *Bromus* had higher concentrations of most elements relative to *Hilaria*. However, this hypothesis alone does not explain why *Bromus* would do better in the presence of *Hilaria*, although it may explain why *Hilaria* biomass is decreased in the presence of *Bromus*.

Scenario 4, Root exudates and hydraulic redistribution: Plants exude carbon, water, and other compounds through their roots. These compounds serve many functions. Many plants exude compounds that increase nutrient availability in soils (e.g., oxalic acid, citric acids) and species growing in calcareous soils exude a greater quantity and more different types of such compounds than plants growing in less alkaline soils (Ström et al. 1994, Gries & Runge 1995, Tyler & Ström 1995). Exudates are also a common response to nutrient stress (e.g. Zhang et al. 1991&1997, Awad et al. 1994, Cakmak et al. 1996, Deubel et al. 2000). It is very possible that *Bromus* can utilize nutrients freed by *Hilaria* root exudates. In fact, given the much higher root CEC of *Bromus* compared to *Hilaria*, *Bromus* is likely to outcompete *Hilaria* for any nutrients in the soil solution. Cannon et al. (1995) found a similar benefit conferred between species as a result of oxalate exudation. In the limited space of our pots, the roots of the two plants would also not be able to avoid each other as they might in nature, and thus such parasitism is highly likely.

Hydraulic redistribution, where water and dissolved nutrients are released at night into the soil, is also a possible explanation of our observations. This process has been demonstrated to operate in desert grasses (Caldwell 1990). The exuded water and dissolved nutrients have been shown to be scavenged by neighboring plants (Caldwell 1990, Dawson 1993, Caldwell et al 1998), and is likely to be especially advantageous for plants with roots concentrated in shallow soil layers (e.g., grasses). This hypothesis and the mycorrhizal hypotheses seem the most likely to explain why *Bromus* benefits from the presence of *Hilaria* and *Hilaria* is disadvantaged by the presence of *Bromus*.

Management implications and future direction

Eliminating *Bromus* from western rangelands is probably not a realistic goal for land managers. However, suppression of *Bromus* during active restoration of natives is likely an achievable end state. Given the vast amount of acreage requiring treatment, any soil amendment chosen will have to be inexpensive and easily applied. This study provides some clues to this optimal amendment, as there is clearly a range of soil salinity within which the native *Hilaria* is not affected or actually benefitted, but that suppresses *Bromus* biomass. Most of our treatments are likely candidates. Most promising appears to be Na_2HPO_4 and K_2HPO_4, both of which greatly stimulated *Hilaria* via the addition of Na^+, K^+, and P, but also suppressed *Bromus*. Additionally, the addition of NaCl alone also warrants further study. We need further research into these additives to find the optimal addition levels for *Hilaria* communities, and to test whether this works in grass communities dominated by other native species. However, the success of these treatments may be overshadowed by the ability of *Bromus* to utilize natives for growth enhancement. We need to understand the nature of this relationship so we may better understand if there is some way to lessen, or short-circuit, the facilitation of *Bromus* by native species.

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Direct effects of soil amendments on field emergence and growth of the invasive annual grass *Bromus tectorum* and the native perennial grass *Hilaria jamesii*

Introduction

Bromus tectorum (cheatgrass) is an annual invasive grass, which is native to Europe, northern Africa, and southwest Asia. However, it is now abundant in several countries around the world and has invaded millions of acres in western North America (Klemmedson & Smith 1964; Mack 1981; Novak & Mack 1993). *Bromus tectorum* invasion can have profound consequences for ecosystems by altering nutrient (Evans et al. 2001) and fire cycles (Whisenant 1989; Peters & Bunting 1992; Grace et al. 2001). In addition, *B. tectorum* can also alter soil food webs (Belnap & Phillips 2001).

The negative impacts of *B. tectorum* invasions have prompted many researchers and land managers to search for effective methods of control. Grazing has been used to control *B. tectorum*; however, it does not appear to be effective (Vallentine & Stevens 1994). Herbicides have also been widely studied but are expensive and detrimental to human and environmental health. Although some herbicides have negative effects on *B. tectorum*, little is know about effects on the native community (Beck et al. 1995). Several species of fungi have been investigated as biological controls; however, their use may be limited and their effectiveness is uncertain (Tranel et al. 1993 a & b; Grey et al. 1995). Despite the use of all these control methods, *B. tectorum* is still abundant throughout North America.

Altering resource availability can alter competition between weedy and desirable plants (Kay & Evans 1965; DiTommaso & Aarssen 1989; Bilbrough & Caldwell 1997; Tilman et al. 1999; Yoder & Caldwell 2002; Lowe et al. 2003) and may be considered a form of biological control (Tilman et al. 1999). Resource biological control is achieved by finding a resource that is limiting for the weedy species but not the desirable species. Carbon (C) amendments (such as sugar, sawdust and wood chips) can reduce soil nitrogen (N) and have been widely used to control annual weeds (McLendon & Redente 1991; Morghan & Seastedt 1999). Although such C amendments can be effective, sugar is very expensive and sawdust/wood chips require significant labor and create large disturbances. Tilman et al. (1999) found that *Taraxacum officinale* was limited by potassium (K); therefore, fertilizers with low K reduced *T. officinale* density by reducing its competitive ability relative to *Festuca rubra*.

In Canyonlands National Park, Belnap and Phillips (2001) documented that *B. tectorum* generally occurs in areas dominated by the native perennial grass *Hilaria jamesii* and only rarely occurs in areas dominated by the natives *Stipa hymenoides* and *S. comata*. Subsequent studies found that the invasion pattern was due to difference in the availability of K and P in the soils (Belnap et al. in review, Newingham et al. in review). Other studies have also found that *B. tectorum* growth is positively associated with K availability (Howell1998, Morrison 2000, Belnap et al. in review). Both magnesium (Mg) and calcium (Ca) can inhibit the uptake of K by plants (Haynes & Goh 1978; Thompson & Troeh 1978; Brady & Weil 1996), and thus K/Mg and K/Ca can determine K availability and thus *B. tectorum* success. *B. tectorum* success is also related to soil phosphorus (P) availability (e.g., P/calcium carbonate [$CaCO_3$], P/manganese [Mn]; Belnap et al. in review; Miller 2000). Calcium carbonate and reactive oxides such Mn, zinc, and iron can bind with P making it unavailable to plants (Latjtha & Schlesinger 1988, Miller 2000). Increased NaCl has been found to reduce K in olive trees (Loupassaki et al. 2002) and Belnap et al. (2003) found *B. tectorum* in laboratory studies to be salt-sensitive, regardless of the type of salt.

Using soil amendments to reduce P and/or K may prove to be an effective method of control for *B. tectorum*. Carreira & Lajtha (1997) found that available P could be reduced in a calcareous entisol by adding soluble $CaCl_2$. They attributed this to Ca-induced precipitation of $CaCO_3$. As discussed above, Mg compounds can reduce plant-available K. On of the most

effective amendments in the previous laboratory study was zeolite, a high-cation exchange capacity (≈220 $cmol_c\ kg^{-1}$), crystalline, hydrated aluminosilicate of volcanic origin (Ming & Mumpton 1989). Zeolite may be pre-charged with certain ions to release them and exchange for other ions in the soil (Williams & Nelson 1997). In the previous laboratory experiment, we had charged zeolite with Na, resulting in this Na being released into the soil in exchange for other cations.

In the following study, we conducted soil amendment experiments to determine whether altering soil chemistry could reduce *B. tectorum* success in the field. For these field experiments, we selected the four amendments that suppressed *B. tectorum* emergence and biomass without affecting *H. jamesii* in the previous laboratory experiment ($CaCl_2$, $MgCl_2$, NaCl and zeolite). We applied them at various concentrations and seeded *B. tectorum* or *H. jamesii* at sites dominated by *B. tectorum* (the situation a restorationist would face).

Methods

Site description: Field experiments were conducted in the Needles District of Canyonlands National Park, Utah (1525 m elevation, average annual precipitation 215 mm). Soils were part of the Begay series and are classified as fine sandy loam. Precipitation events were recorded from September 1, 2001 until June 1, 2003. Soil water content at 10 cm was also recorded with a Campbell data logger (Figure 1).

We collected soils at 0-10 cm depth from around the site (30 subsamples) and analyzed them for texture and chemistry before amendments were applied. Phosphorus (Olsen et al. 1954) and available K (Schoenau & Karamonos 1993) were extracted with $NaHCO_3$. Zinc, Fe, Mn, and copper (Cu) were extracted with diethyltriaminepentaacetic acid (Lindsay & Norwell 1978). All exchangeable cations (Ca, Mg, K, sodium [Na]) were extracted with ammonium acetate ($NH_4C_2H_3O_2$; Thomas 1982). Acid neutralizing potential (the combination of $CaCO_3$ and oxides of Zn, Mn, Fe, and Mg) was measured by HCl neutralization (Allison & Moodie 1965) and thus includes any soil constituents that neutralize acid. Texture was determined by the hydrometer method and total N was determined by Kjeldahl analysis (Bremner 1996). Cation exchange capacity was analyzed by sodium saturation followed by ammonium displacement (Rhoades 1982).

Treatments: We applied field soil amendments at the two sites previously dominated by *H. jamesii* that have been dominated by *B. tectorum* for the past 50 years. At each site we buried PVC pipes (15 cm x 20 cm) to restrain movement of the applied amendments in the soil. Round hardware cloth cages (15 x 46 cm, ¼" mesh) were placed over all plots to prevent rodent herbivory. All amendment concentrations (except zeolite, a solid) were added at equivalent osmolar rates using Cannon et al. (1995) as a guide for additive levels (Table 1). Clinoptilolite (a form of zeolite obtained from GSA Resources, Inc., Tucson, AZ) was charged with Na by equilibration with 2M NaCl for 5.5 days, during which the solution was shaken and replaced every 24 h, and then dried in at drying oven at 60°C. We defined 1x zeolite concentration for this study as that which effectively suppressed *B. tectorum* in the laboratory (Belnap et al. 2003) and used that and other derivative amounts (0.5x, 2x) for this experiment.

Experiment 1 commenced in September 2001 and was harvested in May 2002. We applied deionized water as a control or one of the following 6 amendments: 4x $CaCl_2$, 5x $CaCl_2$, 3x $MgCl_2$, 4x $MgCl_2$, 4x NaCl, and 1x zeolite (7 treatments x 5 replicates x 2 sites = 70 pots). All amendments (except zeolite) were applied in 100 ml of deionized water and 100 ml of deionized water was applied to controls (Table 1). Zeolite was applied in dry form, mixed into the top 1cm of soil, and 100 ml water was added to the pot. After amendments were applied, ten *B. tectorum* seeds were planted, seedling emergence was monitored monthly, and after maximum emergence, seedlings were thinned to 5 well-established individuals. Aboveground biomass was

harvested in just before seed set in May for aboveground biomass, dried at 60°C for 48 hours, and weighed.

Concentration	Amendment	Amount added (mg)
4x	$CaCl_2$	2.4
5x	$CaCl_2$	3.0
3x	$MgCl_2$	3.3
4x	$MgCl_2$	4.4
4x	NaCl	4.0
0.5x	zeolite	50.0
1x	zeolite	100.0
2x	zeolite	200.0

Table 1. Amounts of amendment added per gram of soil for each concentration of amendment. All amendments were applied in 100 ml deionized water.

To assess the residual effects of these amendments, we reseeded the same pots in September 2002, but did not reapply the amendments. Emergence was monitored monthly and seedlings were thinned to five individuals. In May 2003 plants were harvested as stated above.

Experiment 2 commenced in September 2002 and plants were harvested in May 2003. For this experiment, we applied water as a control or one of the following 6 amendments: 5x $CaCl_2$, 4x $MgCl_2$, 4x NaCl, 0.5x zeolite, 1x zeolite, and 2x zeolite (7 treatments x 5 replicates x 2 sites= 70 pots). These pots were planted with ten *B. tectorum* seeds. In addition, we applied water as a control and 5x $CaCl_2$, 4x $MgCl_2$, 4x NaCl, and 1x zeolite to another 50 pots and planted with ten *H. jamesii* seeds. Plants were monitored, thinned, and harvested as in experiment 1.

The NaCl and zeolite were the most effective amendments in both 2001 and 2002. Thus to better understand the effects of our additions on soil chemistry, post-amendment soils for the NaCl treatments were analyzed for all exchangeable cations as described above. We were not able to analyze zeolite-treated soils as it was impossible to separate the zeolite from soil and thus would have only given us amounts in the zeolite/soil mixture. Instead, we conducted a laboratory experiment to determine the effect of zeolite on nutrients in the soil. We placed 30 g of zeolite in 7 x 13 mm mesh polypropylene bags (Spectrum Laboratories) and placed the bags in 1 quart mason jars with 320 g soil and 400 ml deionized water (n=6). Jars were shaken every 2 hours during the daytime for 2 weeks to assure soil stayed in solution. Bags were removed from the jars and rinsed with deionized water. The zeolite and soil were allowed to air dry. In another six jars, we place 320 g soil and 400 ml deionized water with no zeolite. We analyzed the soil for P, available K, NH_4, NO_3, micronutrients (Zn, Fe, Mn, Cu), and exchangeable ions (Ca, Mg, K, Na) in the following treatments: soil + water + zeolite and soil + water. Soil + water values were subtracted from soil + water + zeolite values to determine how zeolite affected soil nutrients.

Statistical Analyses: Biomass data is reported as an average biomass per individual per pot. Total pot biomass showed similar patterns and thus is not presented. Emergence and biomass data were analyzed with a two-way ANOVA with site and amendment as fixed factors. There were no site differences in any analyses; therefore, the two sites were combined and data were

analyzed with a one-way ANOVA. If assumptions were not met, data were transformed or a Kruskal-Wallis non-parametric test was used. Individual amendments were compared to controls using independent samples t-tests. Analyses were run on SPSS version 12. Differences were considered statistically significant at $P<0.05$ unless otherwise noted in the text.

Results

Abiotic conditions

The 30-year average annual precipitation for the Needles District of Canyonlands National Park is 216 mm; however, the total precipitation during experiment 1 (2001-2002, 8 months) was only 55 mm. During the three months (May 2002-August 2002) that lapsed between experiments, Needles received 34 mm of precipitation. Total precipitation was 169 mm during experiment 2 (2002-2003, 9 months) and thus was three times greater than that received during experiment 1 (Figure 1) although it was still below average. Soil water content June 2001 through May 2003 is shown in Figure 1. In the fall when *B. tectorum* germinates, soil water content was higher in experiment 2 than in experiment 1. However, soil water content was much higher during the spring growing season in 2001 (experiment 1) than the spring growing season in 2002 (experiment 2). Soil chemistry characteristics of the experimental site are described in Table 2.

Emergence

Adding soil amendments had a significant effect on *B. tectorum* emergence in experiment 1 (Figure 2a, df = 6, $F = 8.314$, $P < 0.001$). Whereas 4x $CaCl_2$, 3x $MgCl_2$, and 4x NaCl had no significant effect on *B. tectorum* emergence compared to controls, 5x $CaCl_2$, 4x $MgCl_2$, and 1x zeolite reduced *B. tectorum* emergence ($P = 0.07$, $P = 0.03$, $P < 0.001$, respectively). When *B. tectorum* was reseeded into pots without amendments reapplied, amendments had no significant effect on *B. tectorum* emergence (Figure 2b, df = 6, $F = 2.121$, $P = 0.063$). Only the 4x $MgCl_2$ amendment had a significant effect on *B. tectorum* emergence ($P = 0.05$); however, this effect was stimulatory. The amendment 3x $MgCl_2$ show a trend towards increasing emergence ($P = 0.10$).

In experiment 2, adding soil amendments also had a significant effect on B. tectorum emergence (Figure 3a, df = 6, F = 3.796, $P = 0.003$). Adding 5x CaCl2, 4x MgCl2, 0.5x zeolite, and 1x zeolite had no effect on emergence compared to controls. In contrast, 4x NaCl and 2x zeolite had negative effects on emergence ($P = 0.03$, $P = 0.006$, respectively). Soil amendments in experiment 2 also had a significant effect on H. jamesii emergence (Figure 3b, df = 4, chi-square = 20.05, $P = 0.03$), as the NaCl amendment reduced emergence ($P = 0.06$).

Biomass

Soil amendments applied in experiment 1 also had a negative effect on *B. tectorum* shoot biomass in 2001 (Figure 4a, df = 6, $F = 4.125$, $P = 0.001$). As seen for the emergence results, 4x $CaCl_2$, 3x $MgCl_2$, 4x $MgCl_2$, and 4x NaCl had no effect on biomass, whereas 5x $CaCl_2$ and 1x zeolite had negative effects on biomass compared to controls ($P = 0.03$, $P = 0.003$, respectively). Overall amendments in 2002 when *B. tectorum* was reseeded into pots without amendments reapplied, amendments had no effect on biomass (Figure 4b, df = 6, $F = 1.698$, $P = 0.137$). However, in a pair-wise comparison 1x zeolite negatively affected *B. tectorum* biomass ($P = 0.05$).

Overall in experiment 2, applying soil amendments had little effect on *B. tectorum* biomass (Figure 5a, df = 6, $F = 1.859$, $P = 0.09$), as only 0.5x zeolite tended to decrease *B. tectorum* biomass ($P = 0.08$). Soil amendments had no effect on *H. jamesii* biomass (Figure 5b, df = 4, $F = 0.504$, $P = 0.73$), although 1x zeolite showed a tendency to increase *H. jamesii* biomass.

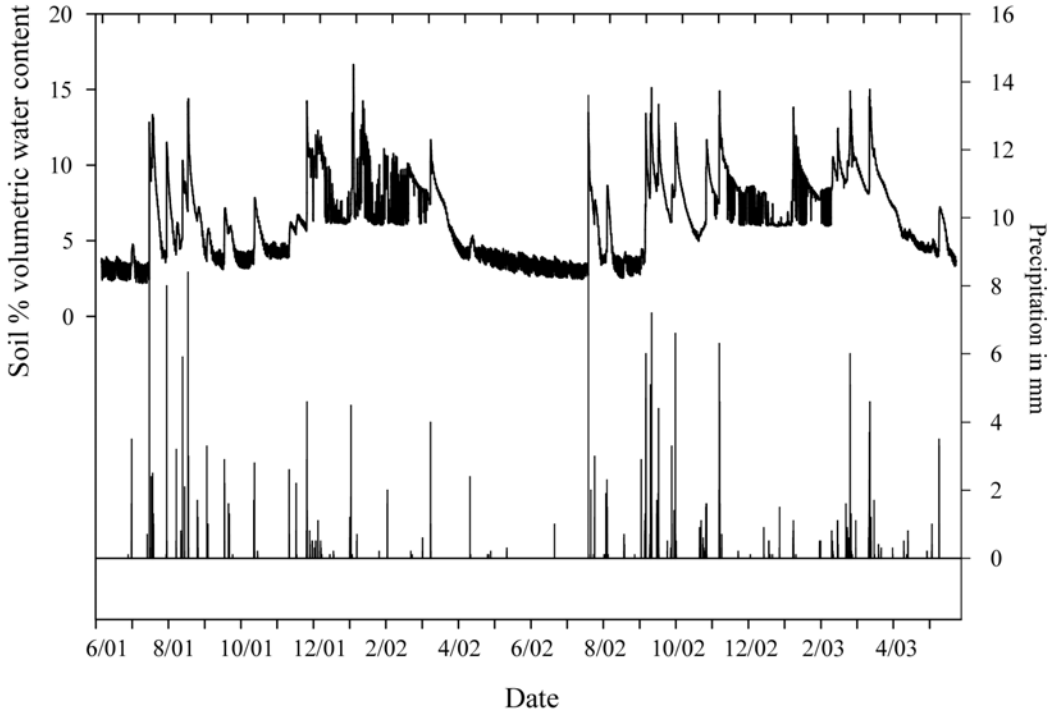

Figure 1. Soil moisture content at 10cm depth and precipitation in Canyonlands National Park from June 2001 to May 2003, which covered the span of the 2001-2002 and 2002-2003 experiments.

	Stipa	*Hilaria*
P (ppm)	5	9
Total N (ppm)	173	179
Available K (ppm)	91	162
Zn (ppm)	0.3	0.3
Fe (ppm)	2.0	2.2
Mn (ppm)	3.2	3.6
Cu (ppm)	0.4	0.5
Exchangeable Ca (ppm)	3146	3179
Exchangeable Mg (ppm)	122	148
Exchangeable K (ppm)	172	266
Exchangeable Na (ppm)	57	58
Acid neutralizing potential (%)	6	5
Sand (%)	73	73
Clay (%)	12	13
Silt (%)	15	15
Cation exchange capacity (EC meq\100g)	5	5

Table 2. Soil chemistry at the study sites in Squaw Flat, Needles District , Canyonlands National Park.

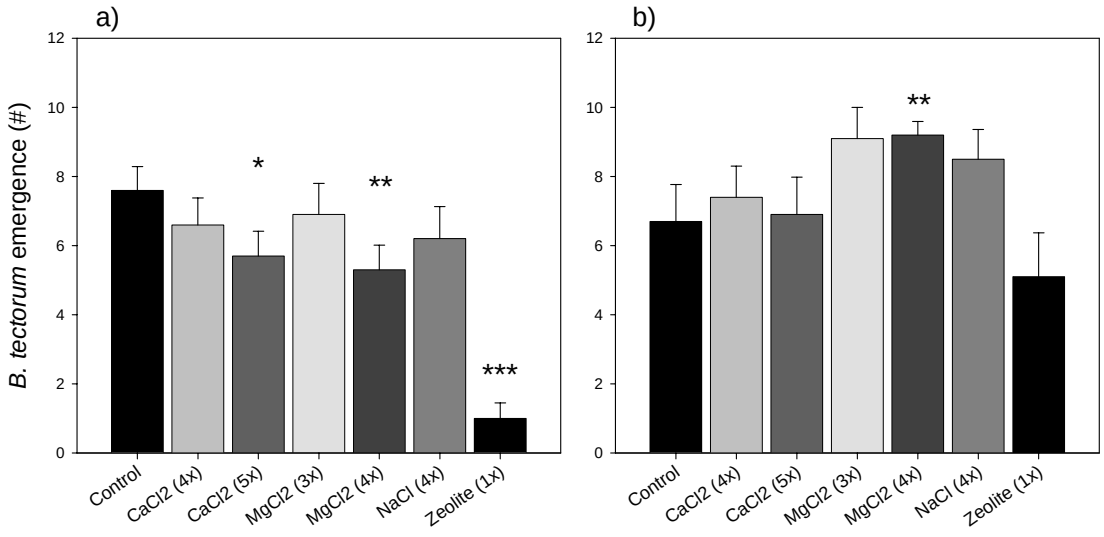

Figure 2. Effects of soil amendments on emergence of *Bromus tectorum* (out of 10) for experiment 1. a) Emergence of *B. tectorum* in 2001 immediately after amendments were applied and b) emergence of *B. tectorum* the following growing season (2002) without additional amendments applied. Numbers in parentheses signify amendment concentrations. Error bars represent ± 1 standard error. * = $P \leq 0.10$; ** = $P \leq 0.05$; *** = $P \leq 0.001$.

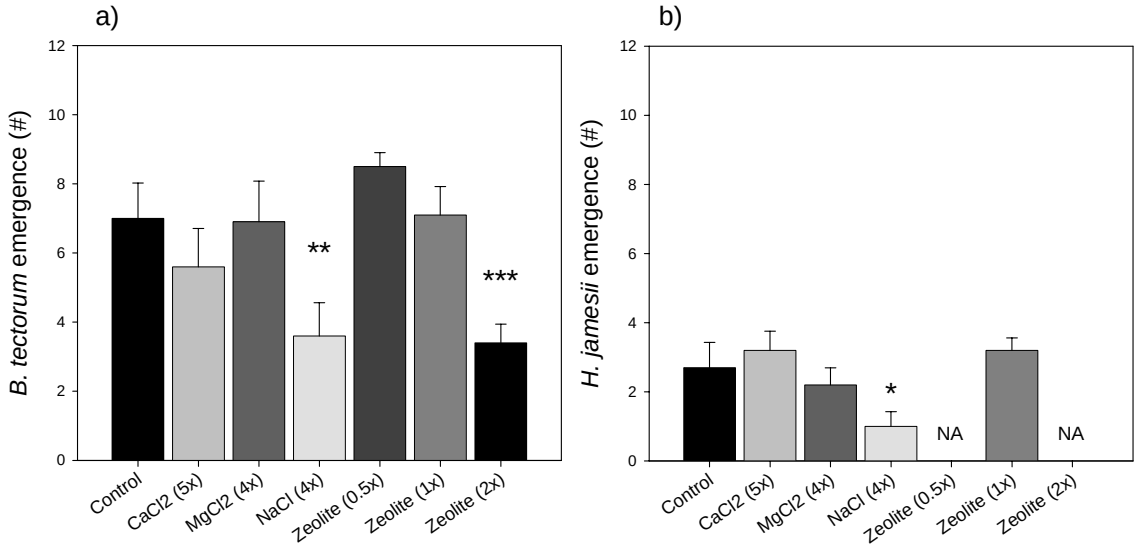

Figure 3. Effects of soil amendments on emergence (out of 10) of a) *Bromus tectorum* and b) *Hilaria jamesii* for experiment 2. Numbers in parentheses signify amendment concentrations. Error bars represent ± 1 standard error. * = $P \leq 0.10$; ** = $P \leq 0.05$; *** = $P \leq 0.001$. NA (not appropriate) signifies amendments that were applied to *B. tectorum*, but not *H. jamesii*.

Changes in soil chemistry after 1 year and effects of zeolite

Exchangeable soil cations in the control and NaCl-treated soils after the second year of experiment 1 are listed in Table 3. The NaCl treatment added 729 ppm Na to the background 58 ppm in the soil, resulting in a total of 788 ppm Na. At harvest two years later, there was 247 ppm Na left in the NaCl treated pots, indicating there had been a 69% decrease two years after application of NaCl, presumably due to leaching. After two years there were also decreases in exchangeable Ca, Mg and K ($P = 0.003$, $P = 0.001$, $P = 0.03$, respectively) in the NaCl treated soils compared to the control.

When we tested how zeolite additions altered soil chemistry, we found the dominant affect to be a large increase in soil Na (Table 4). In addition, the zeolite increased soil Zn, Fe, Mn, Cu, exchangeable Mg, exchangeable K, and NH_4 ($P < 0.0001$, $P = 0.001$, $P = 0.001$, $P < 0.0001$, $P = 0.005$, $P = 0.02$, $P < 0.0001$, $P < 0.0001$, respectively) while decreasing exchangeable Ca ($P = 0.05$).

Discussion

Our goal was to alter soil chemistry in a way that allowed *B. tectorum* to germinate but that suppressed its emergence in a soil currently dominated by *B. tectorum*. Amendments that prevent *B. tectorum* from emerging are essential since *B. tectorum* plants with reduced biomass may still set seed. Several amendments (5x $CaCl_2$, 4x $MgCl_2$, 4x NaCl, 0.5x zeolite, 1x zeolite, 2x zeolite) in our study had negative effects on *B. tectorum* emergence and biomass. However, the same amendment concentration did not always affect emergence and biomass similarly in the different experiments between years. For example, although the amendments and experimental set up were exactly the same, 5x $CaCl_2$, 4x $MgCl_2$, and zeolite 1x negatively affected *B. tectorum* in experiment 1 (2001-2002) but not in experiment 2 (2002-2003). We propose that the higher rainfall during experiment 2 may have leached these amendments more rapidly from the surface soils, and thus application levels may need to be adjusted to match precipitation levels. Changes in humidity and temperature can also affect soil moisture and thus the transport of ions (Zeng et al. 2003).

Time since application also affected our results. In experiment 1, the negative effect of 1x zeolite on emergence seen in experiment 1 was lost after a year of leaching, although there was still some effect on biomass in the second year after application. The addition of 4x $MgCl_2$ suppressed emergence in the first year, but after a year of leaching this amendment actually stimulated emergence.

There were also some unexplainable effects. In contrast to most of the amendments, 4x NaCl had negative effects on emergence in experiment 2 but not experiment 1. In 2002, zeolite 0.5 and 2x both suppressed biomass, whereas 1x zeolite was not different from the control. We cannot readily explain either of these observed effects.

In order for soil amendments to be an effective form of weed control, amendments must be inexpensive and easy to apply at large scales. In addition, these amendments will likely be applied in plant communities where natives still exist and thus these amendment need to have minimal effect on native plants. Our experiments highlight several soil amendments that can reduce *B. tectorum* emergence and biomass without negatively affecting *H. jamesii*. However, between year variability in effectiveness suggests that one must be cautious when applying them, as certain amendments may have negative effects on *B. tectorum* in one year but not effect or even stimulate *B. tectorum* in another year. This year-to-year variability needs to be studied further in regard to the amendment effects on both *B. tectorum* and *H. jamesii* in the years following application. In addition, the effectiveness of a given amendment likely depends on soil type and thus experimentation needs to occur on fine-textured soils as well. In addition, more information is needed on how these soil amendments may affect other native plant and animal species within the community.

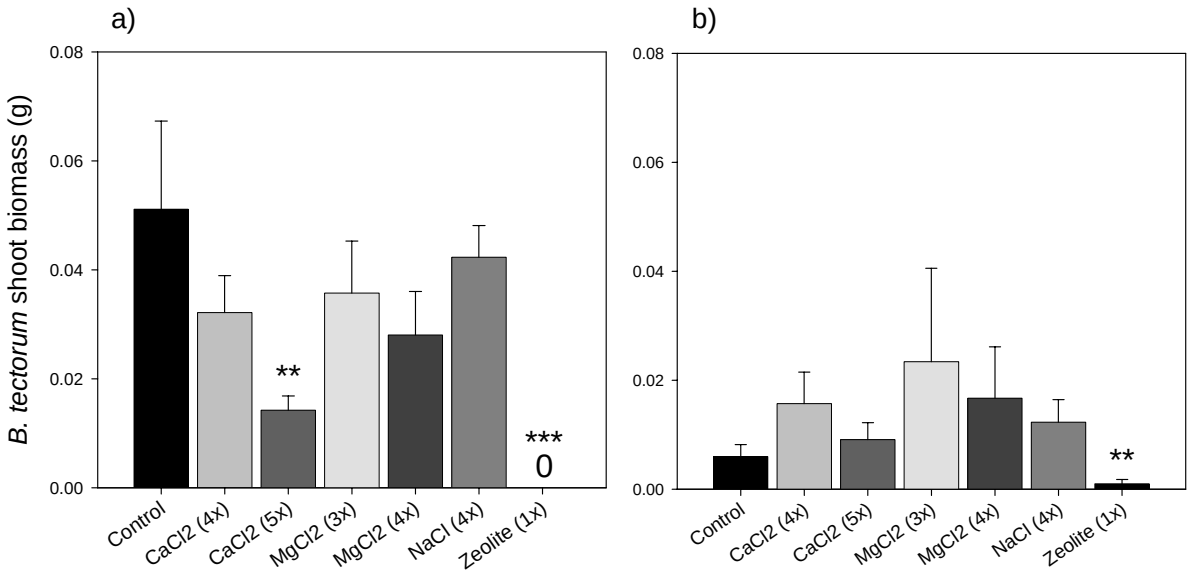

Figure 4. Effects of soil amendments on aboveground biomass of *Bromus tectorum* for experiment 1. a) Shoot biomass of *B. tectorum* in 2001 immediately after amendments were applied and b) shoot biomass of *B. tectorum* the following growing season (2002) without additional amendments applied. Numbers in parentheses signify amendment concentrations. Error bars represent ± 1 standard error. * = $P \leq 0.10$; ** = $P \leq 0.05$; *** = $P \leq 0.001$.

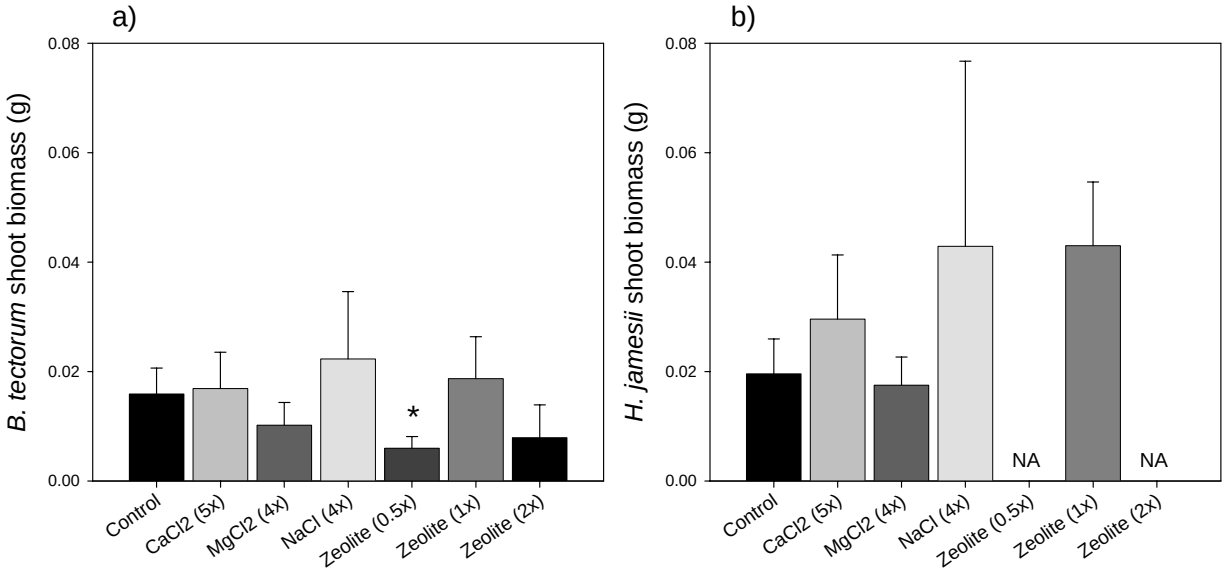

Figure 5. Effects of soil amendments on aboveground biomass of a) *Bromus tectorum* and b) *Hilaria jamesii* for experiment 2. Numbers in parentheses signify amendment concentrations. Error bars represent ± 1 standard error. * = $P \leq 0.10$. NA (not appropriate) signifies amendments that were applied to *B. tectorum*, but not *H. jamesii*.

	Control	NaCl
Na (ppm)	79	247 ***
±	4	24
Ca (ppm)	3690	3133 **
±	77	133
Mg (ppm)	195	150 **
±	9	6
K (ppm)	267	204 **
±	20	16

Table 3. Mean values (± standard error) of exchangeable cations in soil of control and NaCl-treated soils after plants were harvested. ** = $P \leq 0.05$, *** = $P \leq 0.0001$.

	Soil + Water + Zeolite	Soil + Water	Zeolite
P (ppm)	6.2	5.8	0.4
Available K (ppm)	85.9	84.3	1.6
Zn (ppm)	0.6	0.4 ***	0.2
Fe (ppm)	15.6	2.1 **	13.5
Mn (ppm)	50.7	6.4 **	44.3
Cu (ppm)	0.9	0.4 ***	0.5
Exchangeable Ca (ppm)	2695	2937 **	-242
Exchangeable Mg (ppm)	146	127 **	19
Exchangeable K (ppm)	246	206 **	40
Exchangeable Na (ppm)	651	66 ***	584
NH_4	2.5	0.9 ***	1.6
NO_3	0.5	0.8	-0.4

Table 4. Soil chemistry of samples in zeolite laboratory experiment when zeolite and soil are soaked in deionized water or only soil soaked in deionized water. Significant differences between soil + water + zeolite and soil + water treatments are significant at $P \leq 0.05$ (**) or $P \leq 0.0001$ (***). The third column is the difference between column 1 and 2.

Acknowledgements

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Effects of NaCl and NaCl-MgCl additions on *Bromus tectorum* germination

(This material will not be submitted to a journal until further experimentation is conducted)

Abstract

Previous laboratory studies showed *Bromus tectorum* to be much more salt-sensitive than desert perennial grasses. Therefore, we experimented with the effects of NaCl and NaCl+MgCl on the emergence of *Bromus* in the laboratory and in the field. Levels equivalent to the previous laboratory studies were applied to field plots, and emergence of *Bromus* was completely suppressed. Therefore, we experimented with reduced levels of NaCl and NaCl+MgCl (25%, 40%, and 55% of the field levels) in the laboratory. After ten days, over 20% of the 55% treatment emerged, indicating the optimal level for suppression of *Bromus* is greater than 55% of the field levels. However, these amendments need to be approached with caution. In a previous study, a MgCl treatment suppressed *Bromu*s until it was partially leached from the soil, after which it stimulated *Bromus* biomass. Therefore, before using NaCl to inhibit *Bromus,* long-term studies are needed.

Introduction

Our goal was to find amendments that altered soil chemistry in a way that would allow *B. tectorum* to germinate, but suppress *Bromus* emergence in areas dominated by native grasses. (Amendments that prevent *Bromus* from emerging are essential since *Bromus* plants with reduced biomass may still set seed.) Several amendments (5x $CaCl_2$, 4x $MgCl_2$, 4x NaCl, 0.5x zeolite, 1x zeolite, 2x zeolite) in previous studies showed negative effects on *Bromus* emergence and biomass. The pattern of results from this and other previous studies (Section III, Parts 1-3) indicate that *Bromus* was responding to a salt effect rather than to a specific element. Because NaCl is easily and cheaply obtained, we assessed different NaCl and NaCl-MgCl concentrations on the emergence of *Bromus* in the laboratory and the field.

Methods

Field trial: This field trial was placed at a site in Moab, UT. We based our new NaCl additions on the amount of NaCl in the lowest successful NaCl and zeolite treatments in our previous trials. These were 4x NaCl (247 ppm NaCl) and 1x zeolite treatment (517 ppm NaCl). We then selected salt levels 1/3, 2/3 and 3/3 between these two treatments. We also added MgCl to some of the treatments, as it has been reported to exacerbate salt stress. Therefore, our additions were: 1/3 = 338 ppm, 2/3 = 428 ppm, and 3/3 = 518 ppm. We combined each of these NaCl levels with three levels of MgCl2 previously tried (3.3g, 4.4g, 5.5g). We only recorded emergence of *Bromus* due to the extremely low emergence rates.

Lab experiment: Due to the extreme negative effects of our treatments at the field site, we further reduced the 1/3 NaCl and the 1/3 NaCl-3x $MgCl_2$ addition to test *Bromus* emergence in the laboratory. Given the extreme negative effects of all the field treatments, we chose the lowest level applied (1/3 NaCl) to reduce. Because ambient levels of Na were higher at the Moab site versus the Needles site, our 1/3 NaCl treatment resulted in a total of 1333 ppm Na at the Moab site. We dissolved 0%, 25% (333 ppm), 40% (533 ppm), and 55% (733 ppm) of this amount of NaCl in deionized water, along with 3.3 g of MgCl. Soil was collected from the Moab site and placed in 40 cm plastic dishes. Ten *Bromus* seeds were planted in each dish, and they were watered with the appropriate solution. Emergence of the seeds was recorded.

Results and Discussion

Our intention was to find NaCl levels that allowed *Bromus* to germinate, but that killed the emerging seedling. Complete suppression of *Bromus* emergence was seen in our field studies at all NaCl concentrations (Figure 1). Therefore, it appeared that we could apply less NaCl and still accomplish our purpose. However, when we reduced salt levels in the laboratory (25%, 40%, and 55% of the lowest field amount), we found that salt at 55% of the field levels was not sufficient to suppress *Bromus* emergence completely (Figure 2). The presence of MgCl did not affect emergence. Therefore, further experimentation is needed before the optimal salt level for suppression of emergence is found.

However, results reported in Newingham et al. (Section III, Part 3) indicate that using some amendments (e.g., MgCl) may initially suppress *Bromus*, but do not work in the long-term. In that study, we applied MgCl to field plots. Initially, this treatment significantly reduced *Bromus* emergence. However, after one year during which significant amounts of salts were leached from the soil, the remaining MgCl actually stimulated *Bromus* biomass. Although this same phenomena was not observed in the NaCl treatment, this same scenario is obviously possible. Therefore, before NaCl is used to suppress *Bromus*, long-term plots need to be established and monitored.

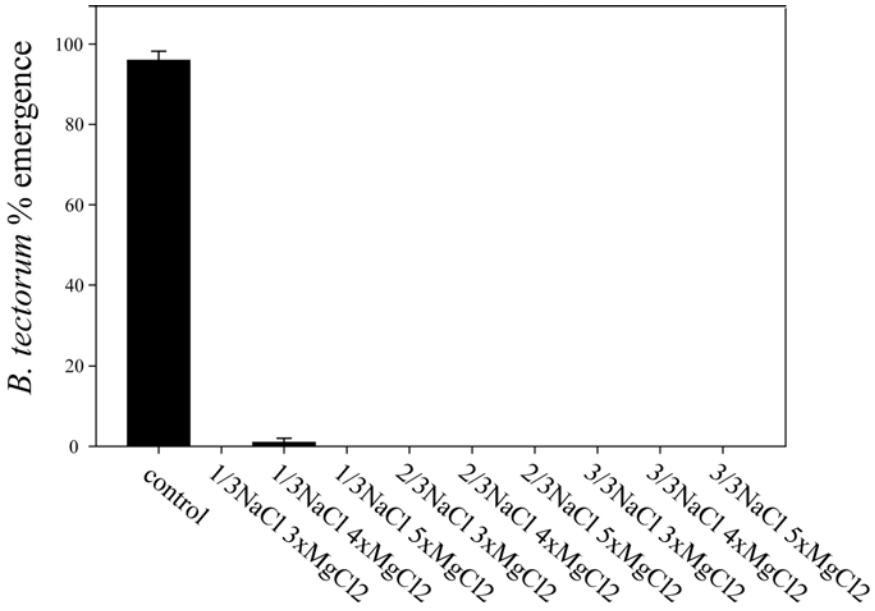


Figure 1. Results of field trial. Note that all NaCl and NaCl-MgCl additions completely suppressed *Bromus* emergence.

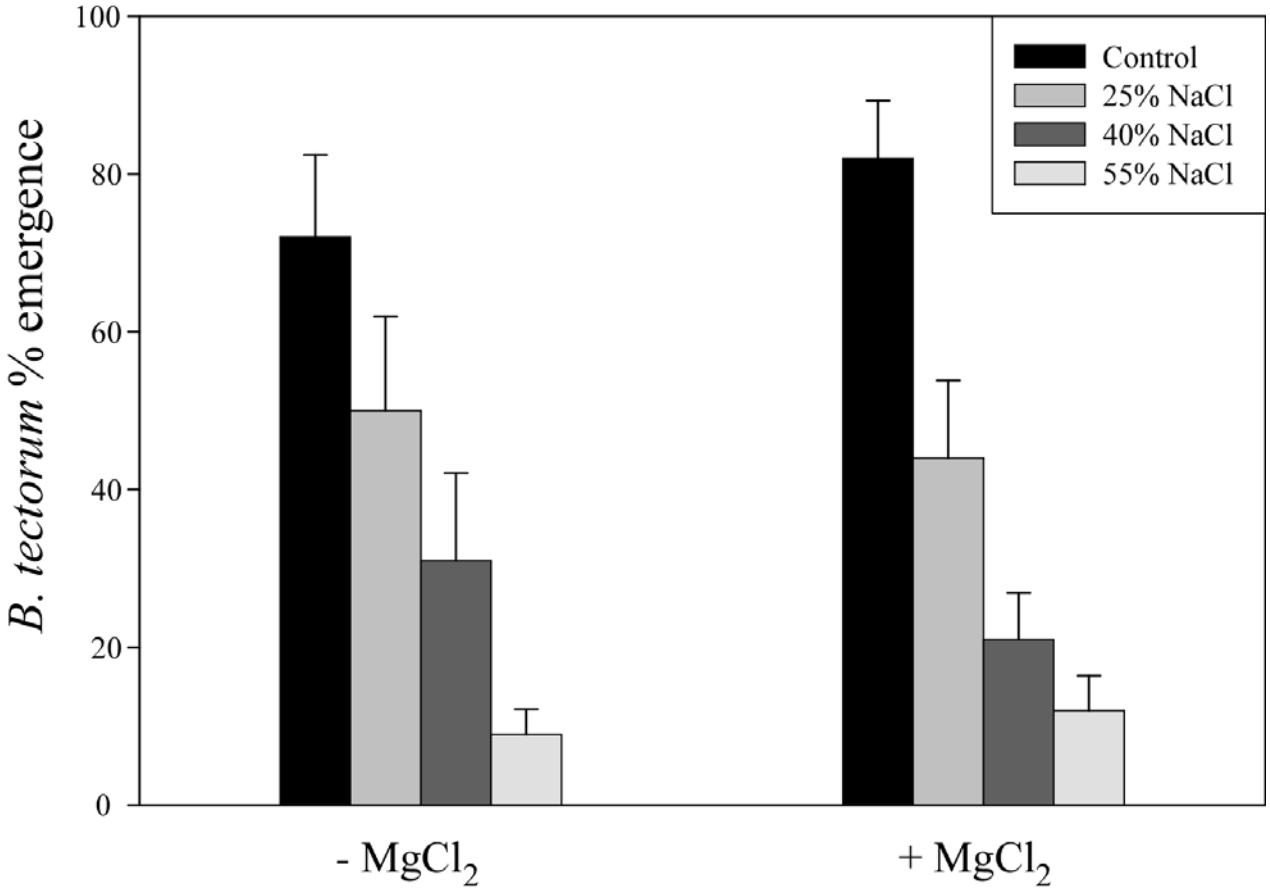


Figure 2. Results from the laboratory trials. After 10 days, even the lowest NaCl level had over 20% emergence, indicating that NaCl levels needed to be slightly higher for complete

Section IV: Once *Bromus* invades, how does it affect native communities and soil nutrient cycles in the absence of other disturbances? Do these alterations affect the ability of the site to support natives?

Effect of *Bromus* invasion on biological soil crusts

Biological soil crusts are an essential part of desert ecosystems throughout the world, as they are important in soil stabilization and soil fertility. The lichens and cyanobacteria in the soil crusts are the main source of nitrogen for this ecosystem. Previously it was thought that these communities showed little change from year to year. However, after seven years of monitoring, we have found the cover of mosses and lichens can increase dramatically over short time periods, often going from just above 0% cover to as high as 9% cover in only six months. During our study time, cover of the nitrogen-fixing lichen *Collema* declined throughout the study, going from 19% in 1996 to as low as 2% in 2003 in response to a large increase in both maximum and minimum temperatures during the study period. Changes in chlorolichen cover (lichens with green algal phycobionts that cannot fix nitrogen), on the other hand, appeared to be driven by precipitation. *Bromus* invasion did not affect species richness in never-grazed plots, but a 50+ year invasion reduced species richness in intermittently-grazed plots. The recent *Bromus* invasion did not affect cover for most species. However, *Bromus* did accelerate the decline in cover of *Collema*. Extended drought resulted in a large decline of all species in 2003. Loss of lichen and moss cover is expected to affect many aspects of this ecosystem. Of special concern is the loss of *Collema*, as it is the dominant source of nitrogen for this ecosystem.

Effect of *Bromus* invasion on vascular plants

We monitored the effect of *Bromus* on two native grass communities (one dominated by the C_4 grass *Hilaria* and the other dominated by the C_3 *Stipa*) for seven years (1996-2003). Grass cover in both communities has been declining since 1996 due to climatic conditions in both the invaded and uninvaded plots. The presence of *Bromus* has not accelerated or slowed this decline. When species lists and richness in the invaded areas are compared to species lists from 1967 and lists from the uninvaded plots, there has been no change in species present. Therefore, we conclude that the presence of *Bromus* has not affected these native plant communities in the absence of grazing and fire.

Effect of *Bromus* on soil phosphorus

Phosphorus (P) is a plant-essential nutrient that is often limiting in the high pH soils found in deserts as it complexes with calcium carbonate and becomes unavailable to plants. Unfortunately, little is known about conditions that free up the unavailable P. In our first set of field measurements, we showed that plant available P changes on a monthly basis. Available P is higher in the winter at sites with Bromus during wet years. However, there is no difference during dry years. We also showed that recalcitrant P has a pronounced annual cycle as well. This was surprising, as this P fraction is considered stable and hence unlikely to increase or decrease in short time periods.

In a second set of field studies, we followed P dynamics after a new *Bromus* invasion. We found that in uninvaded soils dominated by *Hilaria*, there is a weak seasonal pattern of plant available P cycling. In contrast, P in soils dominated by *Stipa* showed very little change through

the year. Interestingly, when either species was invaded by *Bromus*, the amplitude of the positive side of the cycle increases, but there was never less plant available P than when the native species grows alone. In other words, *Bromus* increased plant available P in some seasons (winter), but available P never goes below the native species levels. The severe drought in 2003 dampened the P cycle considerably for both species and for the *Bromus*/native species mix.

Using controlled conditions in the greenhouse, we tested for the effect of *Bromus* on soil P fractions. Surprisingly, plant available P increases when Bromus is grown in the soil, regardless of the soil type. In addition, we found enormous changes in the recalcitrant P with the presence of *Bromus*, suggesting that *Bromus* is able to free up and utilize fractions of P long considered unavailable to vascular plants.

Effects of *Bromus* on nitrogen cycling and decomposition

We measured plant-available nitrogen (N) and plant and soil isotopic composition in soils dominated by *Hilaria* and *Stipa*, with and without *Bromus*. The *Bromus* invasion has significantly altered soil N cycling processes in both native grassland communities. A long-term incubation experiment was conducted to determine the mechanisms for these observed changes. The results of this experiment suggest that different processes are occurring in *Stipa* and *Hilaria* communities that are leading to the same effects as measured by plant-available N availability and stable isotope composition. In *Stipa* communities there is an increase in the amount of labile soil organic N with *Bromus* invasion, coupled with an overall increase in microbial N cycling as measured by both gross and net rates of soil N transformations (mineralization, immobilization, and nitrification). For *Hilaria* communities there was no effect of *Bromus* invasion on labile soil N pools, but as with *Stipa* communities, overall N cycling rates were greater as measured by gross N fluxes. In addition, differences in the stable isotopic composition ($\delta^{13}C$) of *Hilaria* (C_4) and *Bromus* (C_3) allow for the partitioning of microbial utilization between these two substrates.

It was observed that *Bromus* invasion appears to stimulate the activity of at least a portion of the soil bacterial pool which preferentially decomposes *Bromus* litter rather than *Hilaria*. Analyses of soil microbial community structure also indicate that *Bromus* invasion significantly decreases the proportion of fungi in both native communities. This suggests that *Bromus* invasions can significantly alter the composition of the soil microbial community by changing the proportion of soil bacteria to fungi and increasing bacterial activity. These shifts in community structure and substrate utilization lead to increased rates of soil N cycling that, in turn, affect the amounts of plant-available N in these arid grassland ecosystems. In addition, soil nitrogen isotopes may track historical changes following invasion.

Effects of *Bromus* invasion on soil food web structure and growth of natives in soils dominated by *Bromus* for over 50+ years

The presence of the exotic annual grass *Bromus tectorum* altered soil food webs in areas both recently invaded and those invaded for 50+ years when compared to uninvaded areas. Recently invaded soils showed a reduction in both species richness and abundance of soil micro-invertebrates and nematodes, with a more dramatic reduction after 50+ years. Although invaded soils showed an increase in active fungal biomass and active/total fungal biomass when compared to uninvaded soils, species richness of fungi declined. The invasion of *Bromus*, combined with previous livestock grazing, also led to decreased plant species richness. However, despite the depauperate soil fauna, decomposition rates were the same in uninvaded and invaded

sites and soil nutrient availability (e.g., nitrogen) was sufficiently high to support both native and exotic grasses. When seeds of *Hilaria jamesii* were planted into these three soils (uninvaded, recently invaded, invaded 50+ years), germination and survivorship was not affected. Aboveground *Hilaria* biomass in soils dominated by *Bromus* for 5 years was significantly greater than uninvaded soils or those dominated for 50+ years. We attributed the *Hilaria* response to differences in soil nutrients, especially nitrogen, phosphorus, and potassium, as these nutrients were elevated in the soils that produced the greatest *Hilaria* biomass. Thus, despite the fact that *Bromus* significantly altered soil food webs, it did not affect measured soil processes or preclude successful establishment and growth of the native grass *Hilaria*. This suggests that it is not soil species richness *per se* that determines soil process rates or plant success, but instead that the presence of a few critical species can keep the ecosystem function high. However, as the presence of *Bromus* reduces key soil nutrients over time, native plant success may eventually be suppressed.

Conclusions

- In the absence of grazing and fire, *Bromus* did not negatively affect vascular plant communities. Therefore, restoration of invaded grasslands appears to be a reachable management goal, but may require restriction of other disturbances.
- However, *Bromus* did not affect most lichen and moss species. However, it accelerated the decline in cover of the dominant lichen *Collema*. Because *Collema* is the major source of nitrogen for this ecosystem, this is of great concern. Therefore, restoration efforts should include inoculation of this lichen.
- *Bromus* altered soil P. However, changes in soil P appear to be seasonal (winter) and only during wet years.
- *Bromus* increased N availability in the lightly-invaded *Stipa* communities but not in the heavily-invaded *Hilaria* communities. Therefore, these changes are unlikely to favor *Bromus* over natives. However, increased N cycling rates will likely decrease soil N over time
- *Bromus* dramatically altered both the abundance and species composition of soil food webs.
- Site alterations by *Bromus* did not affect the ability of these soils to support growth of the native grass *Hilaria* that once dominated invaded sites. Therefore, managers likely do not need to manipulate soil food webs to successfully restore invaded areas.

Cover of soil lichens and mosses is highly dynamic through time: the effects of climate and the invasion of the annual exotic grass *Bromus tectorum*

Introduction

Biological soil crusts are autotrophic communities consisting of cyanobacteria, mosses, and lichens that occur on soil surfaces throughout the world (Belnap & Lange 2001). In deserts, they can completely cover the large soil interspaces found between plants, and thus are often the dominant living cover found in these regions. Biological soil crusts are a critical aspect of desert ecosystems, as they heavily influence soil fertility, soil stability, and local hydrology. They are often the dominant source of nitrogen (N) for desert plant and soil communities (Evans & Ehleringer 1993; Evans & Belnap 1999) and when wet, they fix carbon (C) at a rate equivalent to vascular plant leaves (Lange 2001). Crust organisms secrete powerful metal chelators to help maintain nutrients in plant-available forms, important in high pH desert soils (Belnap et al. 2001). Crusts reduce wind and water erosion (Warren 2001) and increase soil temperature (Belnap 1995), moisture (George 2000), aeration, and porosity (Harper & Marble 1988). In areas where soils freeze, crusts create a greatly roughened soil surface that increases capture and retention of water (Barger 2003), nutrient-rich dust (Reynolds et al. 2001), seeds, and organic matter (Belnap et al. 2001). Plant productivity and concentrations of most plant-essential nutrients are higher in plants growing in crusted soils compared to adjacent uncrusted soils and plants often have increased survivorship (Belnap et al. 2001). Soil food webs are more complex and organisms more abundant under well-developed soil crusts compared to less developed crusts (Harper & Pendleton 1993; Belnap 2001a).

Soil surface disturbance, such as trampling by livestock, has repeatedly been shown to reduce or eliminate lichens and mosses from soil surfaces (reviewed in Belnap & Eldridge 2001). Other disturbances have also been reported to decrease lichen and moss cover and diversity, including fire and the invasion of exotic annual grasses such as *Bromus tectorum*. Because the degree to which biological soil crusts contribute to a particular ecosystem process depends on the type and amount of crust organisms present, disturbance can have a profound effect on ecosystem function. However, despite the importance of biological soil crusts in general and the importance of their specific floral composition in particular, there have been very few studies of their annual dynamics and factors that control their species composition at a specific locality. To help address this problem, we monitored lichen and moss dynamics in three semi-arid grasslands in SE Utah, USA with different disturbance histories.

Methods

This study was conducted in Canyonlands National Park, 70 km south of Moab, Utah. Three grassland sites were used: Virginia Park (VP), Chesler Park (CP), and Squaw Flat (SF). VP and CP are directly adjacent to each other, but separated by a 100 m tall, 50 m wide rock wall; SF is approximately 5 km away. Sites are at approximately 1700 m elevation. Annual average rainfall is 215 mm, with 35% occurring as summer monsoons (late July-August). Maximum average high temperatures are 20.2^{o} C, while minimum average lows are 3.6^{o} C, with evaporation exceeding precipitation most of the growing season (Fig. 1). During this study period, annual precipitation levels represented below average, above average, and average amounts (Fig. 2). Soils at all three sites are immature, alkaline, well-drained, fine sandy loams derived from calcareous sandstone (Table 1).

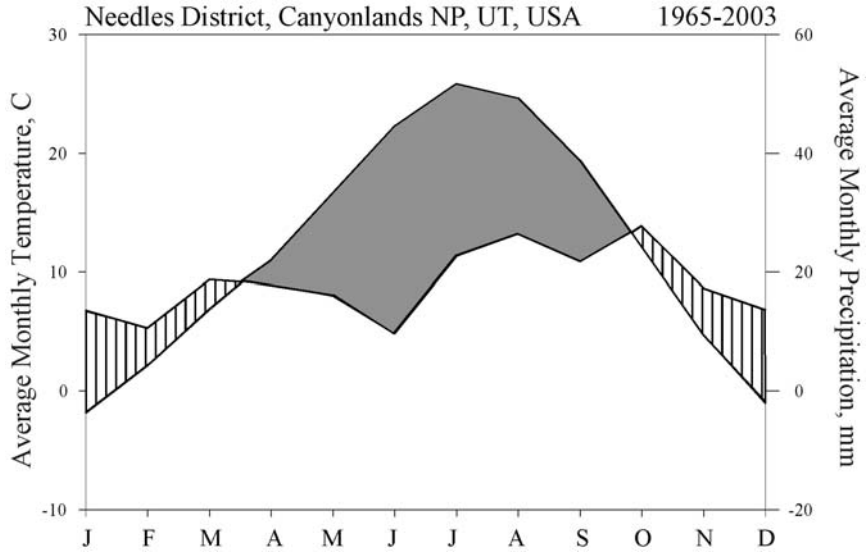


Figure 1. A Walter diagram for the study site area. Note that April-September (six months) are likely times of high water stress for soil surface organisms.

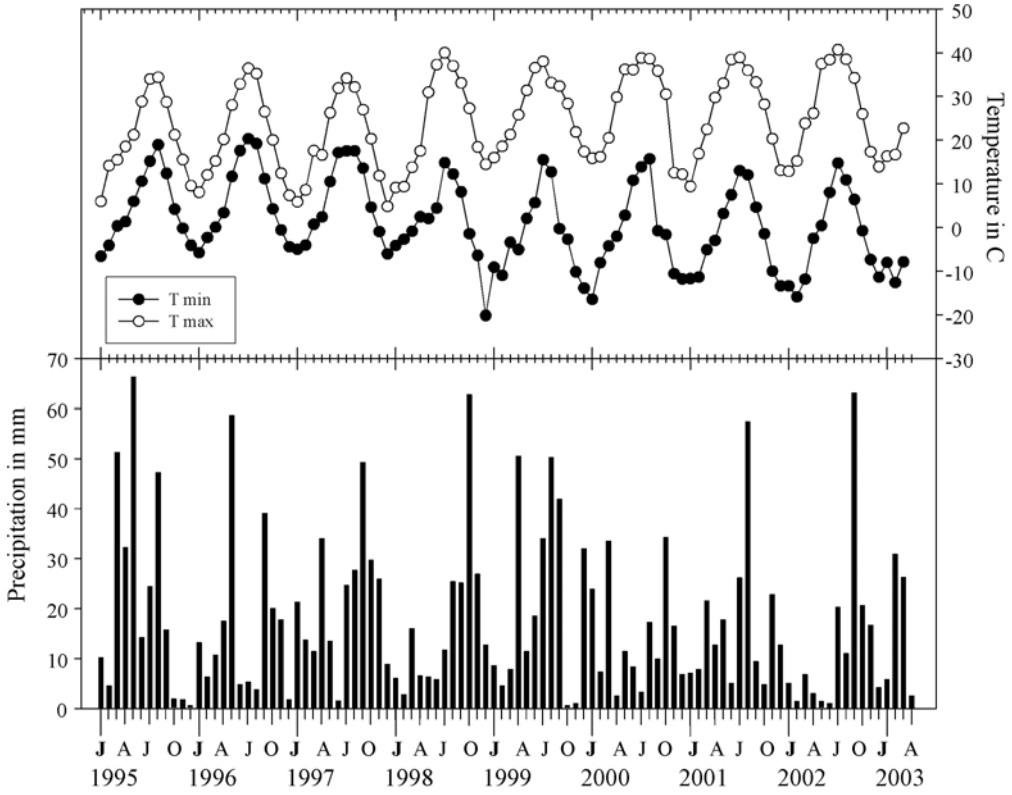


Figure 2. Average monthly maximum temperatures, average monthly minimum temperatures, and total monthly precipitation for the study period. Note the sustained increase in average maximum temperatures after June 1998, especially during winter months, and the sustained decrease in average monthly minimum temperatures.

Site	Plot	% Sand	% Clay	% Silt
VP	H	64.3 ± 1.3	13.7 ± 0.3	22.1 ± 1.5
VP	HB	59.0 ± 0.9	14.7 ± 0.7	26.3 ± 0.5
VP	S	67.7 ± 1.5	13.8 ± 0.4	18.5 ± 1.7
VP	SB	60.0 ± 1.6	14.3 ± 0.3	25.6 ± 1.4
CP	HB	71.3	11.8	16.9
CP	S	71.9 ± 1.6	11.2 ± 0.6	17.0 ± 1.8
CP	SB	71.7 ± 4.6	12.0 ± 1.5	16.3 ± 3.2
SF	HB	70.8 ± 1.3	11.1 ± 0.7	18.1 ± 1.9

Table 1. Means and standard error of soil texture for the different study plots and sites. Sites are VP = never grazed Virginia Park; CP = intermittently grazed Chesler Park; SF = continuously grazed Squaw Flat. Plot types: H = native *Hilaria* plots; HB = native *Hilaria* and exotic *Bromus* plots; S = native *Stipa* plots; SB = native *Stipa* with exotic *Bromus*. Note that there is only one HB plot in CP, and therefore no standard error is reported.

Virginia Park has never been grazed by domestic livestock. Livestock grazing began in this area in the late 1800's. Chesler Park was heavily grazed 2-3 months in winters when there was snow on the ground, which occur every few years. Grazing was removed in 1964. Squaw Flat was heavily grazed in the spring and fall until 1974. Grasslands in this region contain two distinct perennial grassland associations: one dominated by the predominantly spring-active C_3 grasses *Stipa comata* and *Stipa (Oryzopsis) hymenoides* (hereafter referred to as "*Stipa*"), and one dominated by the predominantly fall-active C_4 grass *Hilaria jamesii* (referred to as "*Hilaria*") (Kleiner & Harper 1977, Welsh et al. 1993). Sometime after 1900, parts of CP and most of SF were invaded by the exotic annual cheatgrass (*Bromus tectorum*) which was well established by 1940 (R. Redd, pers. comm.). Virginia Park, although surrounded by areas dominated by *Bromus*, resisted invasion until fall 1994. This invasion occurred mostly in the *Hilaria* communities, although some *Stipa* communities were invaded as well. In spring 1996, permanent 1.0 ha plots were randomly located in *Bromus*-dominated areas in SF and CP and in the two grassland types with and without *Bromus* in VP. In 1998, additional plots were added to CP. Plots were labeled *Stipa* (S), *Stipa/Bromus* (SB), *Hilaria* (H), and *Hilaria/Bromus* (HB). The four plot types were replicated three times in VP (total of 12 plots). In CP, S and HB plots were replicated three times (six plots), while only one SB plot could be established. In SF, HB plots were replicated three times (three plots). This resulted in a total of 22 plots. Six lines were marked every 5 m within each plot, and random points selected along these lines for vegetation and soil sampling.

All sites were sampled yearly in spring, with sites in VP sampled in early fall as well, when soils were dry. There were two core observers throughout the study and in each year one or both of them were present. Double-sampling was frequently employed to make certain that the different observers obtained the same cover estimates. Vascular vegetation is sparse in this area and did not obscure visual identifications. Regardless of plant, litter, rock, lichen and moss cover, there was always at least 15%, and more often 50%, of the soil surface available for new colonization of lichens and mosses. Within each plot, vascular vegetation cover and plant litter

were estimated using 0.25 m^2 nested-frequency quadrat frame and Daubenmire cover classes. Cover of soil lichens and mosses was estimated with a 0.1 m^2 frame containing 20 point hits. These subplots had permanently marked corners so the frame was placed in the same place each sampling time. Thirty sub- samples of the surface 0-10 cm soils were collected randomly each spring, composited into one sample per plot and sent to Brigham Young University Soil Laboratory for texture analyses. These analyses showed soils were very similar among the sites (Table 1). Temperature and precipitation have been collected less than 1 km from the SF sites since 1964.

Statistics were run using SPSS v.11.5 and PCOrd v.4.27. Data were first tested for normality using a Kolmogorov-Smirnov statistic, with a Lilliefors significance level for testing normality. Levene's test was used to examine the equality of variances, and both pooled and separate variance t-tests were used to examine for equality of means. Non-normal data was transformed, or if that was not possible, equivalent non-parametric tests were used. Non-metric multidimensional scaling (NMS) ordination, using Sorenson distance measures, was used to explore the relationship between different lichens and climate conditions. To determine appropriate ordination technique, beta diversity, skewness and coefficient of variation were determined for both columns (species) and rows (plot-year). NMS ordinations were ran with a maximum of 400 iterations and a stability criterion of 0.0001 standard deviations in stress over the last 15 iterations. Each NMS was run at least five separate times to insure pattern stability. The Monte Carlo test was used to test stress and strength of the observed patterns. Pearson *r* and Kendall's tau bivariate correlation statistics were calculated to test relationship between NMS scores and environmental variables.

Speaman's rho rank correlation analyses and stepwise linear regressions models were used to corroborate the NMS results. Other analyses included a general linear model repeated measures that employed both univariate and multivariate analyses and a Type III sums of squares. None of our data met Mauchly's sphericity assumptions and so we used the Greenhouse-Geisser adjustment to validate the univariate F statistic. Between-plot effects were determined with Tukey's Honestly Significant Difference test. The repeated measures analysis was used to test for differences among years and plot type for each species. T- tests were used to compare plots with and without *Bromus* in the same year for the same species. Differences discussed in the text are statistically significant ($P<0.05$) unless otherwise noted.

Results

Climate

Our study sites are in a semi-arid area where potential evaporation exceeds precipitation most of the year (Fig. 1). During our study, climate in this area was highly variable, with maximum temperatures consistently exceeding the 50-year average, especially from 1999-2003, and especially during the winter months of December and January (Fig. 2, Table 2). For instance, the January average maximum temperature during 1995-1998 was 7.3 ^oC, while from 1999-2003, it was 14.1 ^oC. The average maximum for the years 1995 to 1998 was 21.4 ^oC, which increased to 26.9 ^oC from 1999-2003. Minimum temperatures also changed, and were well below the 50-year average for April through October and then much higher than the 50-year average November through March. This was again especially true from 1999-2003, when winter precipitation was substantially below the 50-year average (October through February) and in the

midsummer months of June and July. Therefore, winters during this study were substantially drier and
warmer both day and night than the 50-year average and midsummer months were notably drier, and daytime temperatures hotter, than the 50-year average.

	Average Max. Temperature (F)			Average Min. Temperature (F)			Average Total Precipitation (in.)		
	95-98	99-03	95-03	95-98	99-03	95-03	95-98	99-03	95-03
Jan	1.48	2.86	2.24	0.61	1.34	1.02	0.94	0.75	0.84
Feb	1.17	1.77	1.51	0.63	2.27	1.54	0.64	0.98	0.83
Mar	1.05	1.49	1.29	-0.10	6.10	3.35	1.19	1.02	1.10
Apr	0.93	1.38	1.18	0.97	-1.40	-0.35	1.25	0.79	1.00
May	1.04	1.35	1.19	0.99	0.28	0.64	2.26	0.64	1.45
Jun	1.03	1.18	1.10	0.97	0.63	0.80	0.68	0.85	0.77
Jul	1.03	1.12	1.08	1.02	0.86	0.94	0.73	0.93	0.83
Aug	1.03	1.09	1.06	1.08	0.82	0.95	0.99	1.29	1.14
Sep	1.01	1.19	1.10	1.12	0.25	0.68	1.48	1.42	1.45
Oct	1.06	1.35	1.21	0.91	-0.49	0.21	1.02	0.54	0.78
Nov	1.19	1.48	1.34	0.70	3.35	2.02	1.05	0.83	0.94
Dec	1.57	2.45	2.01	1.09	1.59	1.34	0.43	1.02	0.72
Annual	1.06	1.33	1.20	1.21	-0.40	0.37	1.09	0.08	1.01

Table 2. Ratio of maximum and minimum temperatures and precipitation recorded during the study time to the 50-year average for those same variables.

Virginia Park lichens and mosses

Lichen and moss species richness

Twelve to 13 soil lichen species were found in the VP plots (in approximate order of dominance): *Collema tenax, Aspicilia hispida, Collema coccophorum, Peltula patellata, Psora decipiens, Catapyrenium lachneum, Catapyrenium squamulosum, Heppia lutosa, Toninia sedifolia, Fulgensia desertorum, Fulgensia bracteata, Caloplaca tominii* and *Candelariella terrigena* (Table 3). *Heppia* was not found in the S plots. Four to five moss species were also found (in approximate order of dominance): *Syntrichia caninervis, Bryum argenteum, Syntrichia ruralis, Didymodon vinealis* and *Pterogoneurum ovatum*. *Didymodon* was not found in the S plots. Despite the many species present, soil crusts were heavily dominated by *Collema tenax* and *Syntrichia caninervis*, who individually had higher cover than all other species of lichens and mosses combined.

Climate response

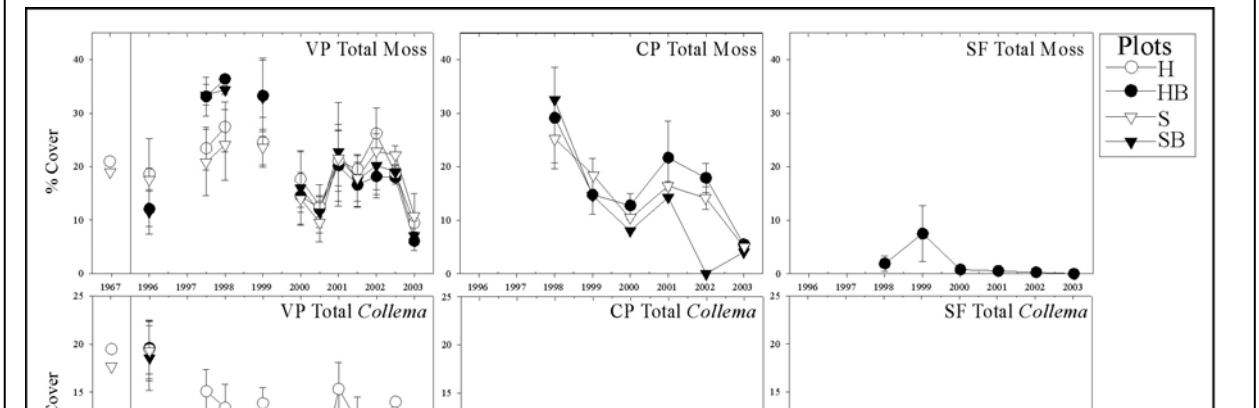
As can be seen in Fig. 3, lichen and moss covers recorded in 1967 (Kleiner and Harper 1977) were within the range of those values recorded in 1996 to 2003. Indeed *Collema* and moss values in 1967 were almost identical to those of 1996, although chlorolichen values were lower in 1967 than in 1996. The cover of total lichens, total mosses, and individual lichen species were surprisingly variable between years, even in the six months between fall and spring. There are several distinct patterns that are evident from these data. Repeated measures analysis shows that the cover of total lichens and *Collema* changed significantly among years and the interaction of plot type and year (data is shown only for *Collema*, as the total lichen patterns are driven by this dominant lichen). Total lichen and *Collema* cover showed a steep decline in 1997 and 2003. In addition, *Collema* cover showed an overall decline in the study period, going from 19% cover in

1996 to only 2-8% cover in 2003. Through time, *Collema* in native H plots had higher cover than the other three plots, which were not significantly different from each other. Lastly, *Collema*

Cyanolichens	VP H	VP HB	VP S	VP SB	CP HB	CP S	CP SB	SF HB
Collema coccophorum	x	x	x	x	x	x	x	x
Collema tenax	x	x	x	x	x	x	x	x
Heppia lutosa	x	x	0	0	0	0	0	0
Peltula patellata	x	x	x	x	x	x	0	0
Green algal lichens								
Aspicilia hispida	x	x	x	x	x	x	x	0
Caloplaca tominii	x	x	x	x	0	0	0	0
Candelariella terrigena	x	x	x	x	0	0	0	0
Catapyrenium lacnhneum	x	x	x	x	x	x	x	0
Catapyrenium squamulosum	x	x	x	x	0	0	0	0
Fulgensia bracteata	x	x	x	x	0	0	0	0
Fulgensia desertorum	x	x	x	x	0	0	0	0
Psora decipiens	x	x	x	x	0	x	0	x
Toninia sedifolia	x	x	x	x	0	0	0	0
lichen sum	13	13	12	12	5	5	4	3
Mosses								
Bryum argenteum	x	x	x	x	x	x	x	x
Didymodon vinealis	0	x	x	x	0	0	0	0
Pteryogoneurum ovatum	x	x	x	x	x	x	0	0
Syntrichia caninervis	x	x	x	x	x	x	x	x
Syntrichia ruralis	x	x	x	x	x	x	0	0
moss sum	4	5	5	5	4	4	2	2
Liverwort								
Riccia sp.	0	x	x	0	0	0	0	0

Table 3. List of lichens and mosses found at the different plots within the study sites (see Table 1 legend for abbreviation definitions).

showed no consistent pattern between spring and fall cover values. Two other cyanolichens



while *Peltula* cover increased in 2002 rather t 001. Both species dropped along with *Collema* in 2003.

Figure 3. Percent cover values for the different lichen species, lichen groups and mosses during a 1967 study (Kleiner and Harper 1977) and this current study time. (See Table 1 legend for abbreviation definitions.)

Cover of total chlorolichens (lichens containing green algal phycobionts) showed a very different response to climate conditions than *Collema*. Repeated measure analysis showed a significant change in chlorolichen cover among years and an interaction of plot type and year. Through time, total chlorolichen cover was significantly highest in H and HB and lowest in SB and S. However, HB was not significantly different from SB. Whereas cover of this lichen group
declined in 1997 and 2003 similarly to *Collema*, cover increased substantially between 1997 and 2002 in contrast to *Collema*. In addition, the chlorolichens often showed relatively large increases in cover in spring relative to the preceding fall cover values, sometimes going from almost 0% to 9%.

Looking at the individual species, *Aspicilia* showed little change over the years in the invaded plots SB and HB. However, in the uninvaded S plots, it showed increases in 1998 and 2002, and in H plots showed an increase in 2002, with the 2002 increase being quite dramatic. Similar to many species, *Aspicilia* dropped drastically in 2003. Overall, *Psora* and yellow lichens (*Fulgensia, Caloplaca,* and *Candelariella* combined) showed little change, although there were a few exceptional years.

Total moss cover showed a different pattern than total lichen cover. Repeated measures analysis showed significant differences among years and plot type x year interaction, although there were no significant cover differences between plot type. In general, moss cover showed a bimodal response to climate, with lower values in 1996, 2000, and 2003 relative to the other years measured. We only collected data on individual moss species in 2002 and 2003. This limited data set shows that the 2003 decline of *Syntrichia caninervis* dominated the response seen in total moss cover (data not shown).

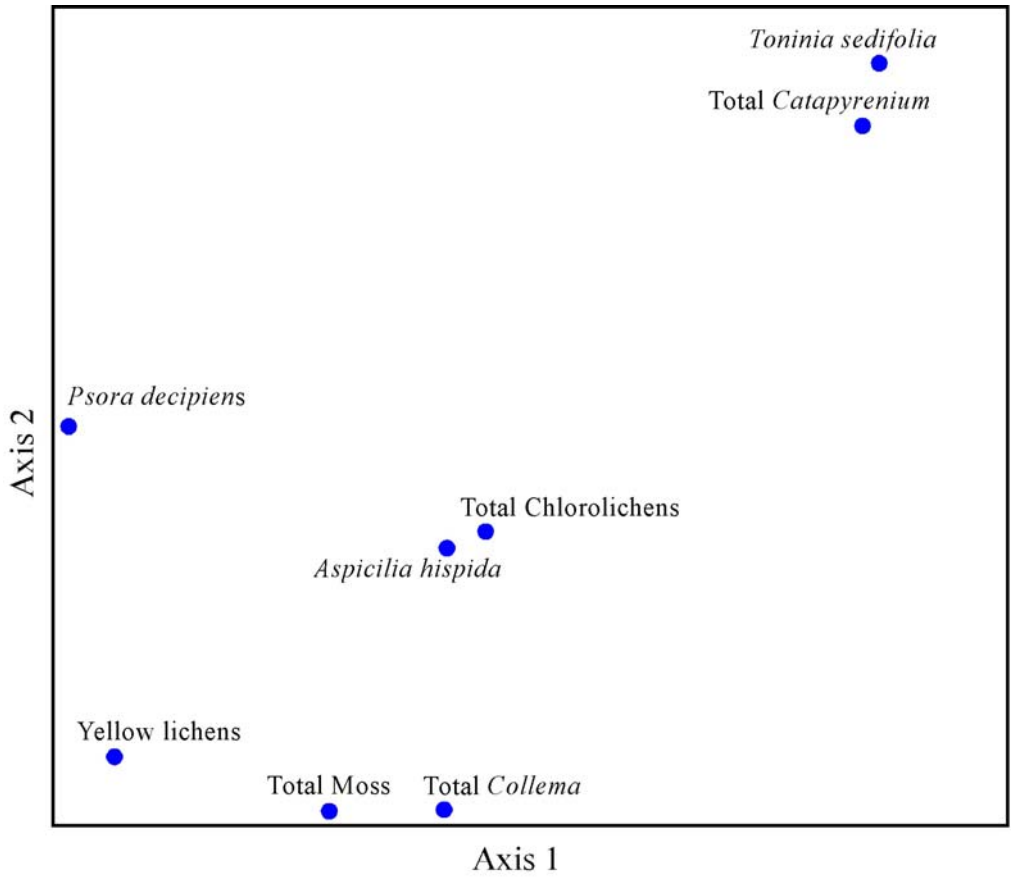
NMS was used to distinguish groups of lichens that responded similarly to precipitation and temperature in the uninvaded H plots and S plots (Fig. 4). These results were similar, and so we only present results from the H plots. NMS showed *Toninia* and the two *Catapyreniums* combined responded similarly fashion, as did moss and *Collema*. *Psora*, *Aspicilia*, and the yellow lichen group were dissimilar from other groups. The moss-*Collema* group and *Aspicilia* responded weakly to average maximum early spring (February; $r = 0.42$) and early fall (August + September + October) average maximum temperatures ($r = 0.4016$; Axis 2). The *Toninia-Catapyrenium* and yellow group were responsive to February precipitation ($r = 0.82$) and March average minimum temperatures ($r = -0.82$; Axis 1) and early spring-late fall average maximum temperatures (Axis 2). *Psora*, on the other hand, responded only to February precipitation and March average minimum temperatures (Axis 1).

The idea that *Collema* and mosses are sensitive to high temperature was corroborated and strengthened with the Spearman's correlation tests between monthly maximum and minimum temperatures with the cover of individual species. Both *Collema* and moss were significantly and negatively correlated with all but one monthly maximum temperature (December for mosses (r values ranged from -0.20 to -0.40 for each month) and October for *Collema* (r values ranged from -0.20 to -0.63 for each month) and positively correlated with all monthly minimum temperatures, although r values were low. On the other hand, chlorolichens as a group and as individual species showed a varied response to maximum or minimum temperatures or precipitation. Rice (1988) suggests running this number of correlations will result in one or two spurious results. However, this would still not invalidate the overwhelmingly consistent pattern in mosses and *Collema*. Stepwise linear regression models also showed that maximum

temperatures were negatively related with *Collema* (r^2 = 0.69) and moss cover (r^2 = 0.48), whereas chlorolichen cover was controlled mostly by precipitation variables (r^2=0.59).

Response to *Bromus tectorum* invasion

Overall, the response of lichen and moss cover to the *Bromus* invasion was limited. Lichen and moss species richness in VP did not appear to be affected. There was some effect on cover: *Collema* and total lichen cover (which was driven by *Collema* cover) was lower in HB



plots than H plots in all years except 1998 and 2000. In 2002, *Aspicilia* cover was lower in both

Figure 4. Ordination of lichen species, lichen groups and total moss using the non-metric multidimensial scaling technique (NMS). Axis 1 is most correlated with February precipitation (*r*=0.82) and March average minimum temperature (*r*=-0.82). Axis 2 is most correlated with average maximum February temperature (*r*=0.42) and the combination of August, September and October maximum temperatures (*r*=0.16).

SB and HB plots when compared to S and H plots, respectively. The liverwort *Riccia* sp. was found only in the invaded plots and not in the uninvaded plots. There were no other significant differences in lichen or moss cover between the S and SB plots, and no significant differences for any other individual lichen species, lichen groupings, individual moss species or moss groupings.

Chesler Park and Squaw Flat lichens and mosses

Lichen cover and species richness were much lower in CP than VP during the study period (Table 3). In CP, four to six species of lichens were recorded compared with 12-13 species in VP. Relative to VP, *Catapyrenium squamulosum, Caloplaca*, *Candelariella*, *Toninia, Heppia*, or either *Fulgensia* were missing from CP. In addition, *Peltula* was missing from the SB plots and *Psora* was not found in either the SB or HB plots in CP. For the species present, cover was always lower than cover for the same species in VP. Like VP, *Collema* cover in CP declined steadily from the initial measurement time until 2003. *Aspicilia* in CP showed similar increases and declines as *Aspicilia* in VP. The presence of *Bromus tectorum* had no obvious impact on the annual cover dynamics of the recorded species. However, it appears to have reduced species richness in CP, as the number of lichens went from six to four species and mosses from four to two species when the S and SB plots were compared. The lack of H plots in CP precluded comparisons with HB plots in CP.

Similar to lichens, moss species richness was reduced in CP (two to four species) compared to VP (five species). *Didymodon* was lacking in all plots. *Syntrichia ruralis* and *Pterogoneurum* were both missing in the SB plots. However, in contrast to lichens, moss cover was as high or higher in CP than VP, with a similar, though not as distinct, bimodal pattern. As with lichens, there was no obvious impact of *Bromus tectorum* on the annual dynamics of total moss cover, although species richness was reduced in the SB plots relative to S plots.

Lichen and moss richness and cover was extremely low in the *Bromus*-dominated SF plots. There were only three lichen species, *Collema tenax*, *Collema coccophorum*, and *Psora*, and only two moss species, *Bryum* and *Syntrichia caninervis*. Although cover was extremely low, these species all showed similar annual cover dynamics among themselves. As we did not measure any uninvaded plots in SF, we cannot report on any effects of *Bromus*.

Discussion

Cover changes in lichen and moss species

The general impression among both scientists and the lay public is that lichens and mosses are slow-growing and thus slow to respond to changing conditions. This study clearly shows this is not always the case. At these sites, large changes in cover were recorded both within and among years. The largest within-year changes in cover were shown by the chlorolichen group, which repeatedly increased from almost 0% cover in fall to up to 9% cover in spring, showing an amazing ability to recover from unfavorable circumstances. Most species and groups showed the ability to increase cover by more than 200% or more in six months. How such rapid growth occurs is puzzling, as the green algae required for establishment of new individuals are limited in these soils (Grondin and Johansen 1993). It is possible that extreme desiccation after a long hot summer results in shrinkage of these organisms, or they may pull themselves down into the soil, becoming difficult to detect. However, this would require the unlikely ability to "ignore" the large summer monsoonal rains that occur in this region. Mosses also showed the ability to dramatically increase cover between years, increasing 20% in both the SC and HB plots from 1996 to 1997.

There are very few published studies with which to compare these results. The only one known to us is an extensive vegetation monitoring program in Australia that includes lichens and mosses and was reported by Rosentreter et al. (2001). In this study, some plots showed little variation in cover over the eight years reported, whereas other plots showed a gradual, but

substantial increase in cover. One plot (on granitic soils) had a tremendous increase in cover in two consecutive years. However, the authors reported that the observed increases in cover were due to a reduction in vascular plant cover such that the mosses and lichens were more visible, as opposed to a real increase in crust cover. While this may have been the case in this study, our results suggest that such increases are certainly possible within short time frames.

Climate response

Different lichens showed various responses to the wide range of climate conditions that occurred during this study. The large declines in *Collema* cover occurred in both *Bromus*-invaded and uninvaded plots, across wet and dry years, and in the absence of soil surface disturbance. Therefore, this decline was most likely due to temperature changes. This was corroborated with the NMS, Spearman's correlations, and stepwise regression analyses. All three indicated that *Collema* is intolerant of the increasing maximum and minimum temperatures that occurred during our study period (Fig. 2, Table 2). Because *Collema* is a gelatinous lichen that readily absorbs water, any size rainfall event will initiate respiratory C losses (in contrast to other lichen growth forms which are slightly hydrophobic and shed small rain events). It takes *Collema* up to 60 minutes in light to compensate for this loss with newly fixed C (Lange et al. 1998). As higher temperatures likely result in both quicker drying and higher respiration rates, the likelihood of C deficits in this lichen increase as temperatures increase. Interestingly, the C_3 grasses at this site declined during this time as well (Belnap et al, in prep). Declines in C_3 grasses were recently noted in the shortgrass steppe, and was attributed to an increase in nighttime temperatures and thus respiration rates (Alward et al. 1999). Thus, it may be that cover of both *Collema* and C_3 grasses decline when temperatures increase due to increased respiratory losses. As *Collema* is the dominant source of N for these grasslands, the loss of this species is likely to have profound consequences for N cycles (Evans and Belnap 1999; see Ecological Implications section below).

In contrast to *Collema*, the chlorolichens showed times of increase during our study, especially during years of higher precipitation. Our NMS correlation and regression analyses suggest these lichens respond mostly to precipitation, while tolerating the higher temperatures that negatively affected *Collema*. Moisture control of the chlorolichens is also supported by the large seasonal swings seen in their cover. Cover was repeatedly low during the post-summer sampling (Fig. 3), indicating that these species are fairly intolerant of dry conditions. However, they recovered rapidly during winter when more moisture was available.

It also has long been believed that mosses and lichens are more tolerant of long-term drought than vascular plants. However, our results suggest that this also may not be true. Chlorolichens seemed to drop even with the short-term droughts encountered during some summers. Although most lichen species and total lichens tolerated the drought years of 2001 and 2002, most moss and lichen species succumbed to lack of precipitation and higher temperatures by 2003. Vascular plants in this area showed a similar response, with most C_3 species able to resist the effects of drought until 2003, when they also experienced a similar, severe drop in cover (Belnap et al. in prep). C_4 species, on the other hand, do not appear to have been affected by this drought.

Response of lichens and mosses to grazing and Bromus invasion

The vascular plant communities in VP, CP, and SF were once quite similar (H. Redd, pers. comm). With constant spring grazing, the perennial grass species in SF were eventually lost and replaced with *Bromus*. In CP, some perennial grass species have also been lost, but only

from small areas that are now dominated by *Bromus*. In VP, no perennial plants have been lost since the *Bromus* invasion (Belnap et al., in prep). Unfortunately, we have no records of lichen or moss cover in SF or CP pre-grazing. However, if the crust communities were once similar as were the vascular plant communities, then CP and SF have clearly lost many lichen and some moss species over the past 100 years. Virginia Park has more than twice as many lichen species as CP (12-13 versus 4-6 species, respectively), and more lichen species were found in CP than SF (4 to 6 versus 3 species, respectively). Mosses were also highest in VP (five species), intermediate in CP (two to four species) and lowest in SF (two species). Compared to VP, there has also been a dramatic reduction in lichen cover in CP and SF. Moss cover, however, was about equal in VP and CP, although greatly reduced in SF relative to both CP and VP.

So which forces were responsible for this loss of species and lichen cover, the impact of grazing or the invasion of *Bromus*? And why has moss cover not been affected in CP? While there is no definitive answer to these questions, there are a few clues. Grazed, but uninvaded plots in CP (H and S plots, Fig 3) show a reduction in species richness relative to VP (12-13 lichen species versus 6 lichen species, 5 versus 4 moss species). There are a few grazed, but uninvaded S sites left in SF and they are almost exclusively covered by cyanobacteria (Belnap, pers obs). This indicates that the dramatic drop in species richness was due to grazing. In addition, the more heavily-utilized SF plots also show a greater decline in species numbers than the less heavily-used CP plots. The idea that grazing may be mostly responsible for the loss of lichen and moss species is not a surprising finding, as soil surface disturbance, especially trampling by livestock, has repeatedly been shown to decimate lichen and moss richness (reviewed in Belnap and Eldridge 2001).

Separating the effect of grazing and *Bromus* invasion on lichen and moss cover is more complicated. Before the decline of lichen cover from drought in all 2003 plots, ungrazed plots in CP consistently supported less lichen cover than VP, and plots in SF had much lower cover than either VP or CP. This indicates both the intermittent winter grazing in CP and the continuous spring-fall grazing in SF was responsible for the decline of lichen cover. Moss cover, on the other hand, was not affected by the intermittent grazing in CP, whereas it was greatly reduced under the more continuous grazing in SF. Mosses often occur under the plant canopies, where they are partially protected from trampling by livestock and thus have had more propagules to recolonize the trampled interspaces once livestock was removed. Observers in other habitats have also noted that after removal of livestock, lichen cover stays suppressed while moss cover recovers more quickly (Rosentreter, pers. comm.)

What has been the effect of *Bromus* on lichens and mosses? In VP, our data do not indicate that *Bromus* has had a large additional negative effect on lichen and moss species richness. However, cover of *Collema* and *Aspicilia* has been reduced with *Bromus* invasion. This reduction in *Collema* cover with *Bromus* was also seen in CP during 1999 and 2000, but not in other years. *Bromus* invasion also appears to have exacerbated the loss of species begun by grazing in CP. Invaded SB plots have lost two of the six lichen species and two of the four moss species found in the S plots. It is not known if this reduction in species richness is solely due to *Bromus* or an interaction between *Bromus* and grazing. Unfortunately, we do not have any H plots in CP to compare to our HB plots. In SF, we again lack H plots and thus it is impossible to know if the far lower lichen and moss richness and cover in the HB plots, relative to VP or CP, are due to heavier grazing or from the longer-term or more extensive dominance of *Bromus*.

Based on the results of this study, *Bromus* invasion has a less dramatic effect on lichen

and moss communities than other studies have reported (Rosentreter 1992, Belnap et al. 1994, Kaltenecker 1997, Kaltenecker et al. 1999, Belnap & Phillips 2001). However, the changes we have documented, especially reduction in the cover of the nitrogen-fixing lichen *Collema*, are expected to have large and widespread consequences for these ecosystems (see below).

Ecological implications for soil fertility and stability

Aside from loss of biodiversity, the loss of lichens and moss cover can have a dramatic effect on ecosystem function in deserts. Loss of lichens and mosses decrease soil stability from wind (Belnap 2001b) and water (Warren 2001) erosion, thus reducing soil fertility. Lichen and moss biological soil crusts have greater soil aeration, porosity, and soil aggregate stability than cyanobacterial soil crusts or bare soil (Belnap 2001c). Soil temperatures under mosses and lichens are up to 14 ^{o}C higher than under bare soil or cyanobacterial soil crusts (those lacking mosses and lichens; Belnap 1995), affecting C and N fixation, nutrient cycling, nutrient availability, and plant nutrient uptake and growth rates. Soils covered with lichens and mosses are rougher than soils lacking them, enhancing water, nutrient-rich dust, and organic matter capture (Harper & Marble 1988, Reynolds et al. 2001).

Because the lichen *Collema* has a higher fixation rate than cyanobacteria (Belnap 2002) and can be the dominant source of N for these ecosystems (Evans and Belnap 1999), the loss of *Collema* is expected to result in drastically reduced N inputs into underlying soils. Nitrogen losses also increase when soil lichens and mosses are lost, as soil loss during high-intensity rain events is greater from less-stable cyanobacterial soil crusts than the more-stable lichen-moss soil crusts (Barger 2003). With higher N inputs and lower N losses, total soil N is higher under *Collema* crusts than cyanobacterial soil crusts (reviewed in Belnap 2001d). In 1999, Evans and Belnap found VP soils had higher soil N and lower delta N in plants and soils when compared to CP, and attributed this difference to the loss of *Collema* cover due to livestock grazing.

Lichens and mosses also fix more C than cyanobacteria (Jeffries et al. 1993). Low levels of soil C in deserts often limit microbial activity and thus rates of decomposition and nutrient cycles (Whitford 2002). Much of the fixed N and C is immediately leaked into the soil and made available to associated organisms, including vascular plants and microbes (Belnap et al. 2001). Therefore, the soils under lichen-moss crusts support a greater abundance of soil food web organisms and a more complex soil food web structure (reviewed in Belnap 2001a). A greater abundance of soil food web organisms is expected to result in faster decomposition rates, greater soil nutrient availability (Whitford 2002), and higher nutrient concentrations in vascular plant tissue. Indeed, plants growing in lichen-moss soil crusts have higher levels of many plant-essential nutrients (Harper & Belnap 2001) than those growing in cyanobacterial crusts or bare soil (reviewed in Belnap et al. 2001).

Conclusions

Given the importance of soil lichens and mosses to soil stability and fertility in many ecosystems around the world, it is unfortunate that we know so little about what affects their population dynamics. This is especially true in light of their apparent sensitivity to changing climate conditions. This study showed that several of the common assumption about mosses and lichens may not be true, including that they grow very slowly and are extremely tolerant of drought. Because various species perform different functions in a given ecosystem, it is also important that we begin to understand more about specific species that comprise biological soil crusts, rather than considering soil crusts as one “thing”.

Acknowledgments

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Effects of a *Bromus tectorum* invasion on a never-grazed grassland plant community

(This material will be combined with all the other information on Virginia Park [soil food webs, nutrient cycling] and submitted to Ecological Monographs)

Abstract

The effect of the invasion of *Bromus tectorum* on two native grass communities (one dominated by the C_4 grass *Hilaria* and the other dominated by the C_3 *Stipa*) has been documented for seven years since the invasion (1996-2003). Grass cover in both communities has been declining since 1996 due to climatic conditions in both the invaded and uninvaded plots. The presence of *Bromus* has not accelerated or slowed this decline. When species lists and richness in the invaded areas are compared to species lists from 1967 and lists from the uninvaded plots, there has been no change. Therefore, we conclude that the presence of *Bromus* has not affected these native plant communities.

Introduction

Virginia Park is a never-grazed grassland inside Canyonlands National Park. Although surrounded by areas invaded by *Bromus tectorum* for over 50 years, this exotic annual grass was not able to extensively invade this area until the fall of 1994. The cause of the invasion appears to have been highly unusual weather patterns during late August and early September, the time that *Bromus* germinates.

We began monitoring the effects of this invasion in the spring of 1996. Since that time, we have followed the impact of *Bromus* on many ecosystem components, including vascular plants and plant surface litter.

Methods

Canyonlands National Park (~1500 m above sea level) is located in a cold semiarid desert in southeastern Utah (avg. annual precipitation is 214 mm and annual average temperature is 11.6 ºC). This area has experienced substantial turnover of its landscape to communities dominated by *Bromus*. When *Bromus* invaded the never-grazed grassland of Virginia Park, it invaded in distinct patches, with the bulk of the invasion occurring on soils dominated by the perennial native C_4 rhizimatous grass *Hilaria jamesii* (hereafter referred to as *Hilaria*). These soils are slightly finer-textured and generally have higher levels of available potassium (K), phosphorus (P), and micronutrients than soils dominated by other native grasses found in this area. Soils dominated by pure stands of *Stipa comata* and *S. hymenoides*, on the other hand, were either uninvaded or only lightly invaded.

In 1996 we laid out three replicate 30m x 30m plots within four vegetation types: uninvaded *Hilaria* (H plots), invaded *Hilaria* (HB plots), uninvaded *Stipa* (S plots) and invaded *Stipa* (SB plots). We have sampled these plots each spring beginning in 1996. At each sample time, vegetation cover by species was sampled in 25 0.25m^2 quadrants within each of the 12 plots. Air temperatures as well as the timing and size of precipitation events were continuously recorded during the sampling times.

Results

Climate: Since 1996, Virginia Park has experienced extreme drought as well as years of both above-average and average precipitation (Figure 1). Air temperatures were also unusual during this time, as they increased throughout the sampling time.

Vascular Plant Litter: Ground litter generally increased with the invasion of *Bromus*. However, ground litter did not build up in the *Bromus*-invaded patches, as was expected (Figure 2). Instead, litter values followed precipitation levels. The same result was found for total (standing plus ground) litter: the presence of *Bromus* increased values in most years, and again, rather than increasing over time, litter values fluctuated with precipitation. Despite high cover values in some years, *Bromus* cover did not drive the patterns seen in either the ground or total litter across the plots. Rather, total litter values appeared to reflect mostly those of the native grasses present (*Hilaria* and *Stipa*). Ground litter, on the other hand, did not follow the pattern of any of the plant species.

Vascular Plant Cover: Cover of specific plants and plant groups changed markedly through time.

Grasses: *Bromus* cover responded readily to precipitation patterns with huge swings in cover from year to year (0-58% cover)(Figure 3). *Hilaria* and *Stipa* both showed fairly steep declines from 1996-2003 in the plots where they were dominant, regardless of invasion status (note, however, that the H plots had very low cover of *Stipa* and the S plots had very low cover of *Hilaria*). The initial decline was not related to precipitation, but appears related to temperature. The declines in *Stipa* during 2002 and 2003 were clearly driven by the extreme drought conditions in this area during this time. As would be expected for a C_4 grass, *Hilaria* did not decline as much as *Stipa* due to drought. Neither species showed a significant response to the presence of *Bromus*. *Sporobolus*, another C4 grass, actually increased during the time of study, despite the increasing temperature and drought, and did not show any effect due to the *Bromus* invasion. (However, note the very low cover of *Sporobolus* in the plots). When cover of all the perennial grasses was combined, a severe decline in cover from 1996 to 2003 can be seen, regardless of the presence of *Bromus*.

Shrubs and Cacti: There were only two species in this category in the plots and their cover was very low (Figure 4). *Atriplex canescens*, a C_4 shrub, showed little response during the measurement time. Cover in the H plots declined steadily throughout the measurement time. Whereas cover did not change in the HC plots, it was extremely low during all years. Cover in the S plots appeared unaffected by the drought, but the presence of *Bromus* did appear to effect cover in the SB plots, with a sudden drop in 2001 and a further drop in 2003. Other shrubs show no consistent response to invasion, and cover in most also dropped in 2003. *Opuntia* showed no effect of drought or *Bromus* invasion during the measurement time.

Herbaceous Annuals: Only one herbaceous annual species had sufficient cover to report separately (Figure 5). *Plantago patagonica* was slightly lower in the *Bromus* invaded plots, especially in 2001, when cover in the two uninvaded plots showed a marked increase not reflected in the invaded plots. The drought of 2002-2003 resulted in zero cover. Other forbs show a similar response spike in 2001 and to drought in 2002-2003. In addition, they also showed a slight reduction in cover in the invaded plots.

C_3 Plants, C_4 Plants, and Total Vascular Plant Cover: When all the C_3 plants were grouped, a dramatic decline over the sample time was observed, although there was a temporary recovery of cover in 2001 (Figure 6). When C_4 plants were combined, no consistent change in cover was observed, as would be expected given their water use efficiency and thus drought

tolerance. Total vascular plant cover stayed more or less steady until the drought of 2002 and 2003 resulted in a decline from 40-80% cover to only 10% or less cover.

Species and Species Richness: A list of species in Virginia Park was recorded in 1967 by Kleiner and Harper (1977), with *Hilaria* and *Stipa* communities listed separately. When the 1967 species list in these two communities is compared to species observed during our sample time, no loss of species has occurred with the invasion of *Bromus*, and therefore no change in species richness was observed.

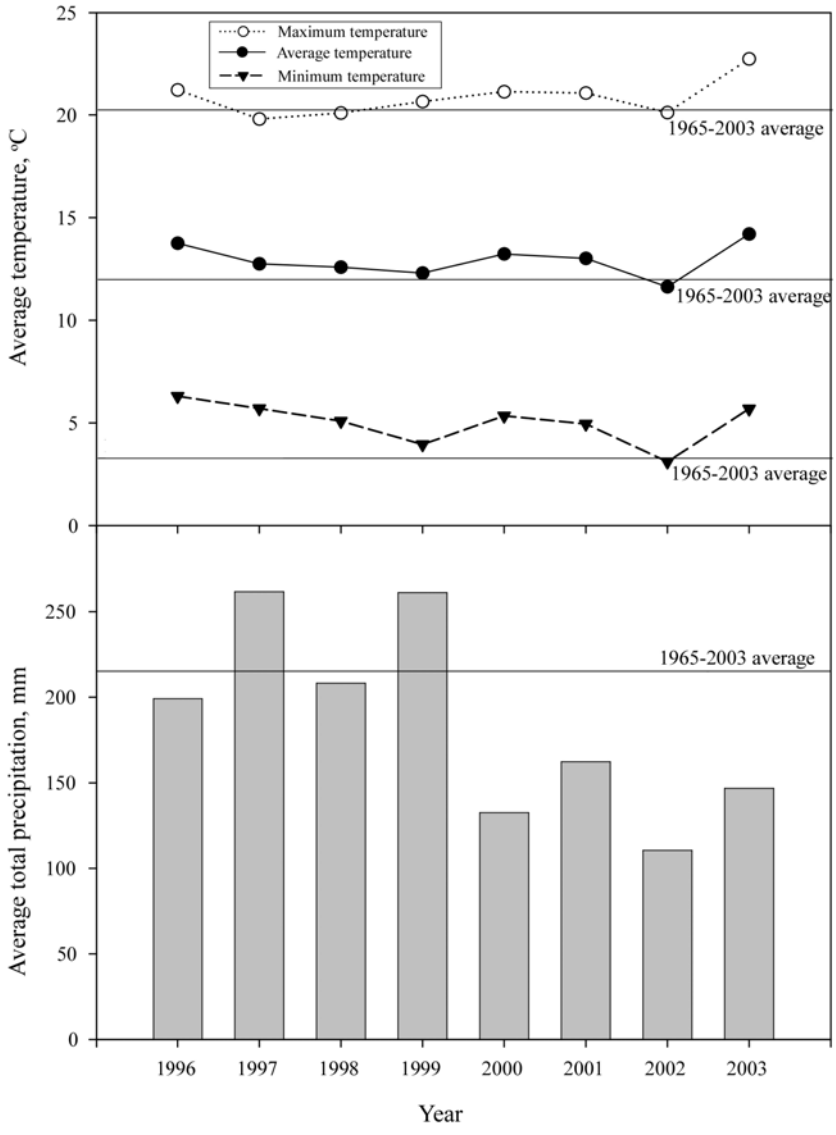


Figure 1. Monthly temperature and precipitation during the study time (1996-2003). The solid lines in the figure represent the 50 year average.

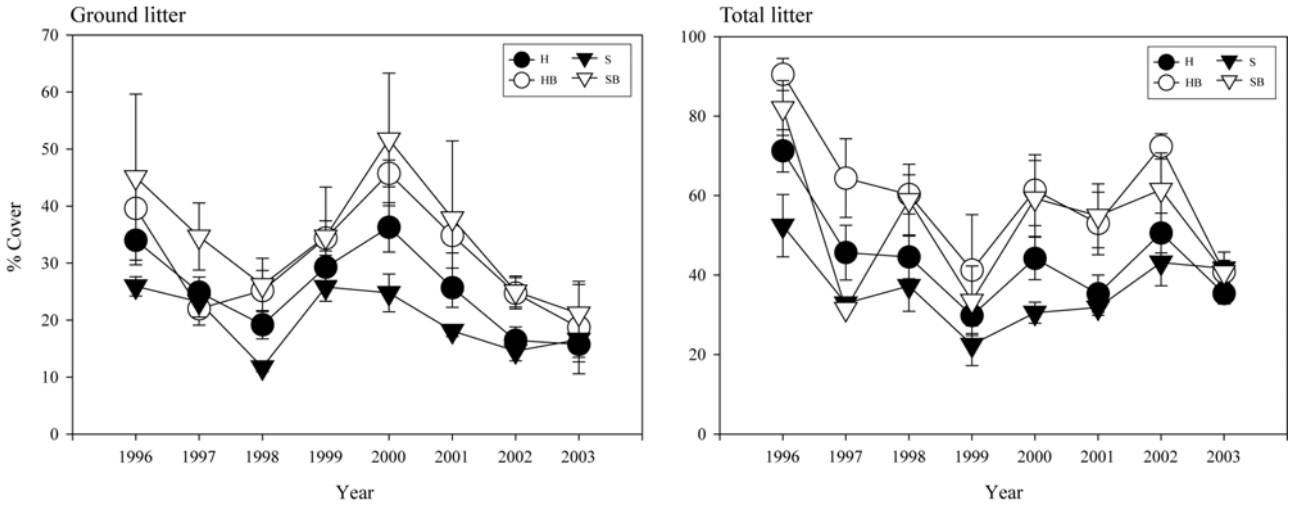


Figure 2. Cover of vascular plant litter during the study time (1996-2003).

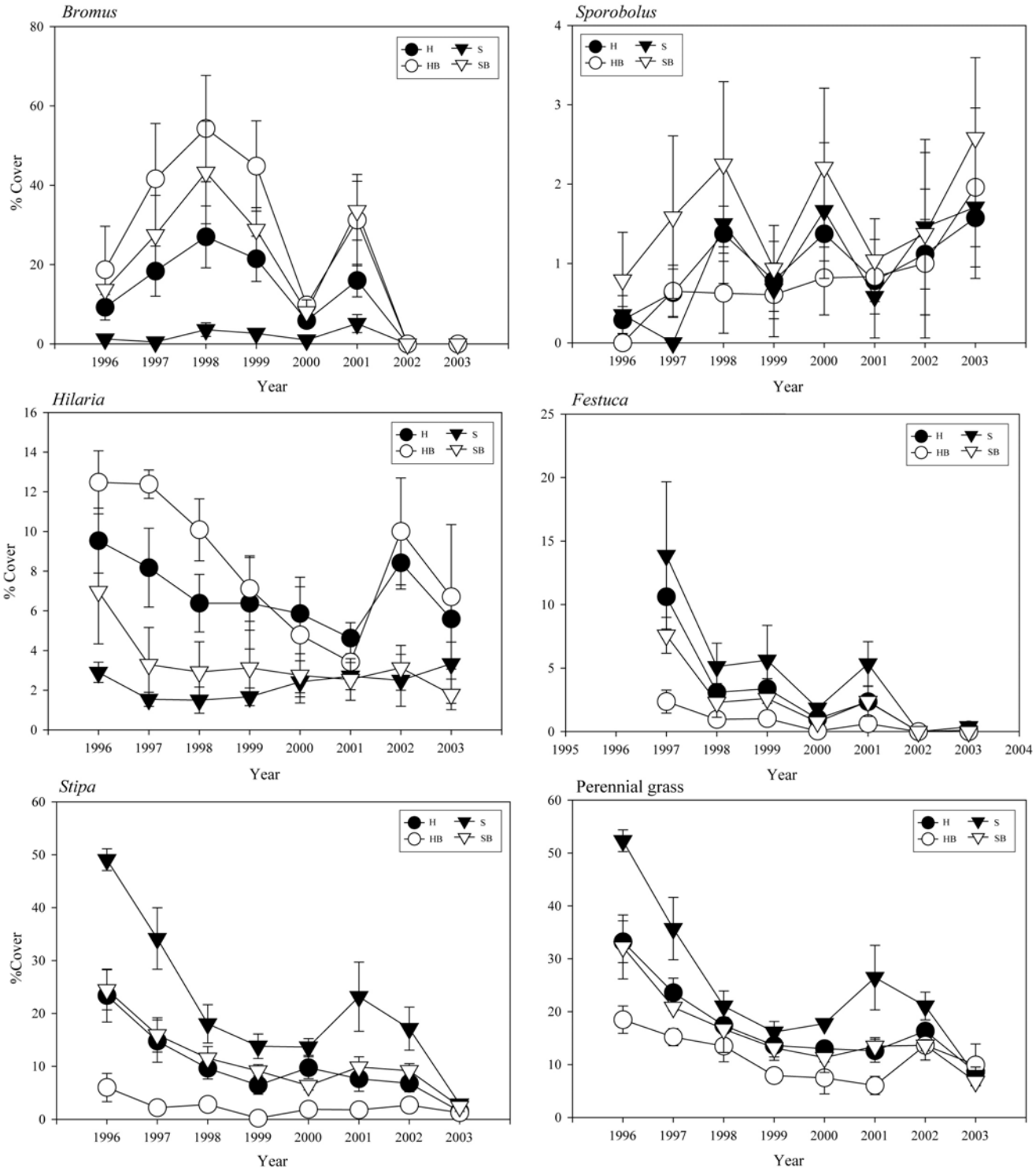


Figure 3. Cover of grasses during the study time (1996-2003).

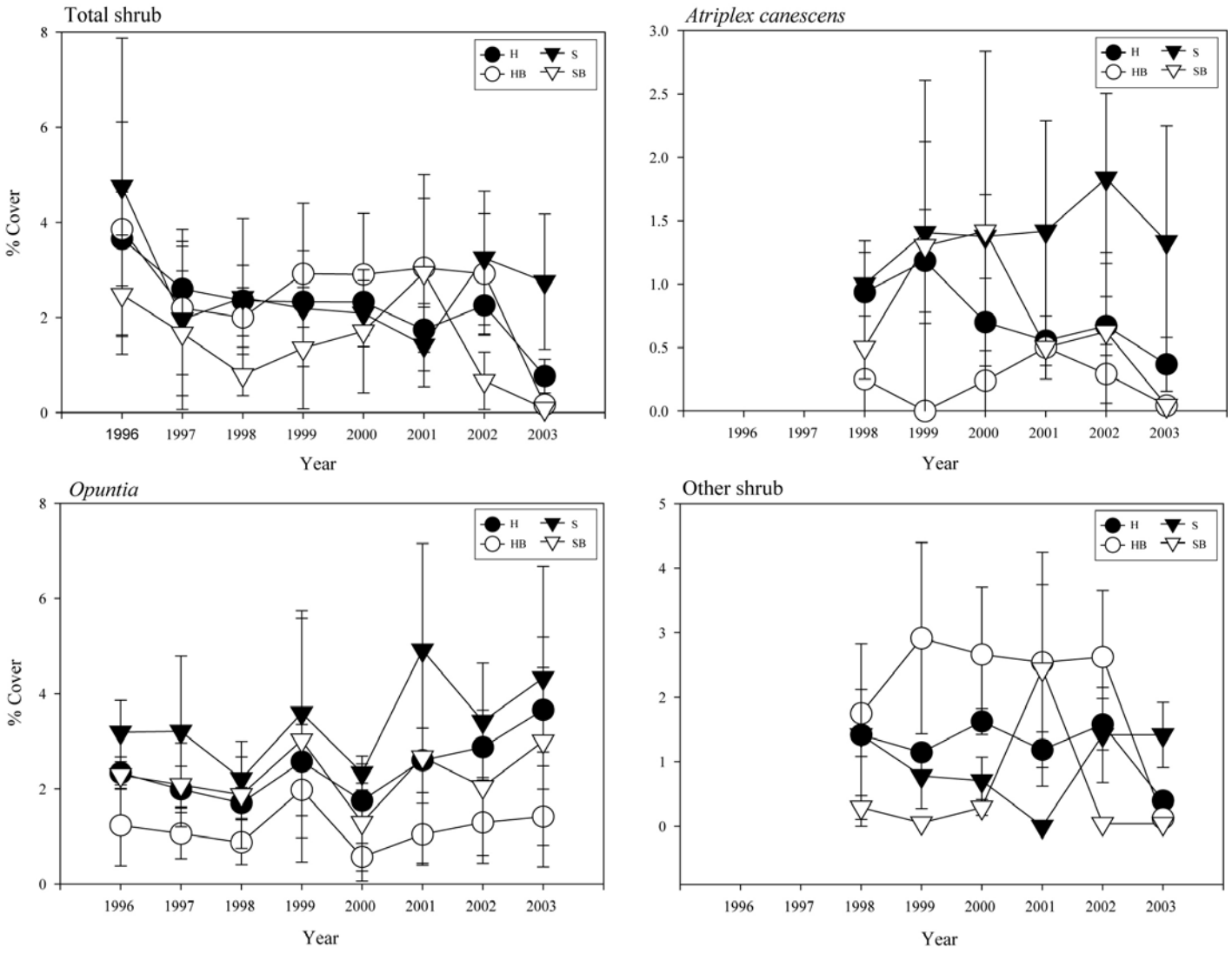


Figure 4. Cover of shrubs and cacti during the study time (1996-2003).

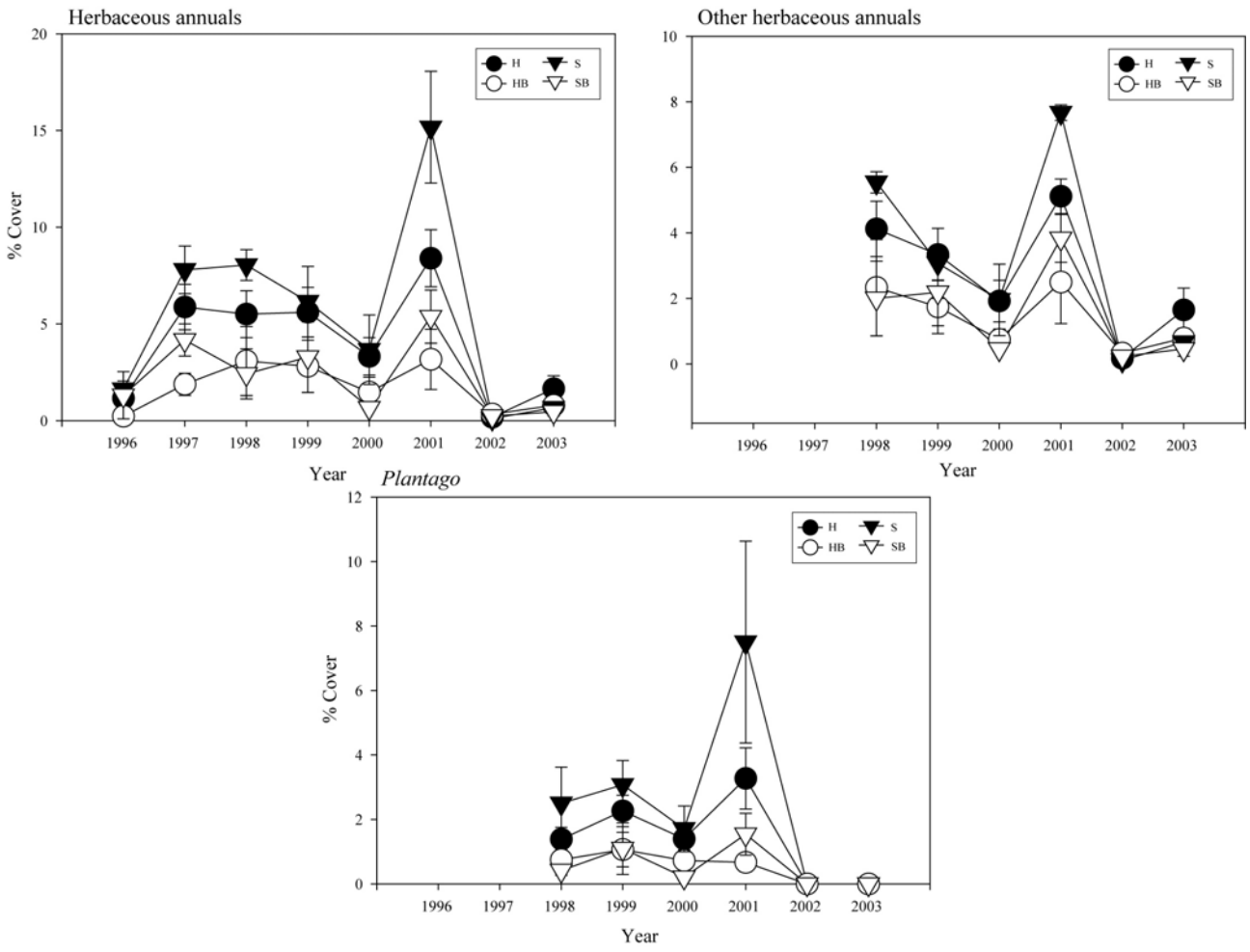


Figure 5. Cover of herbaceous annuals during the study time (1996-2003)

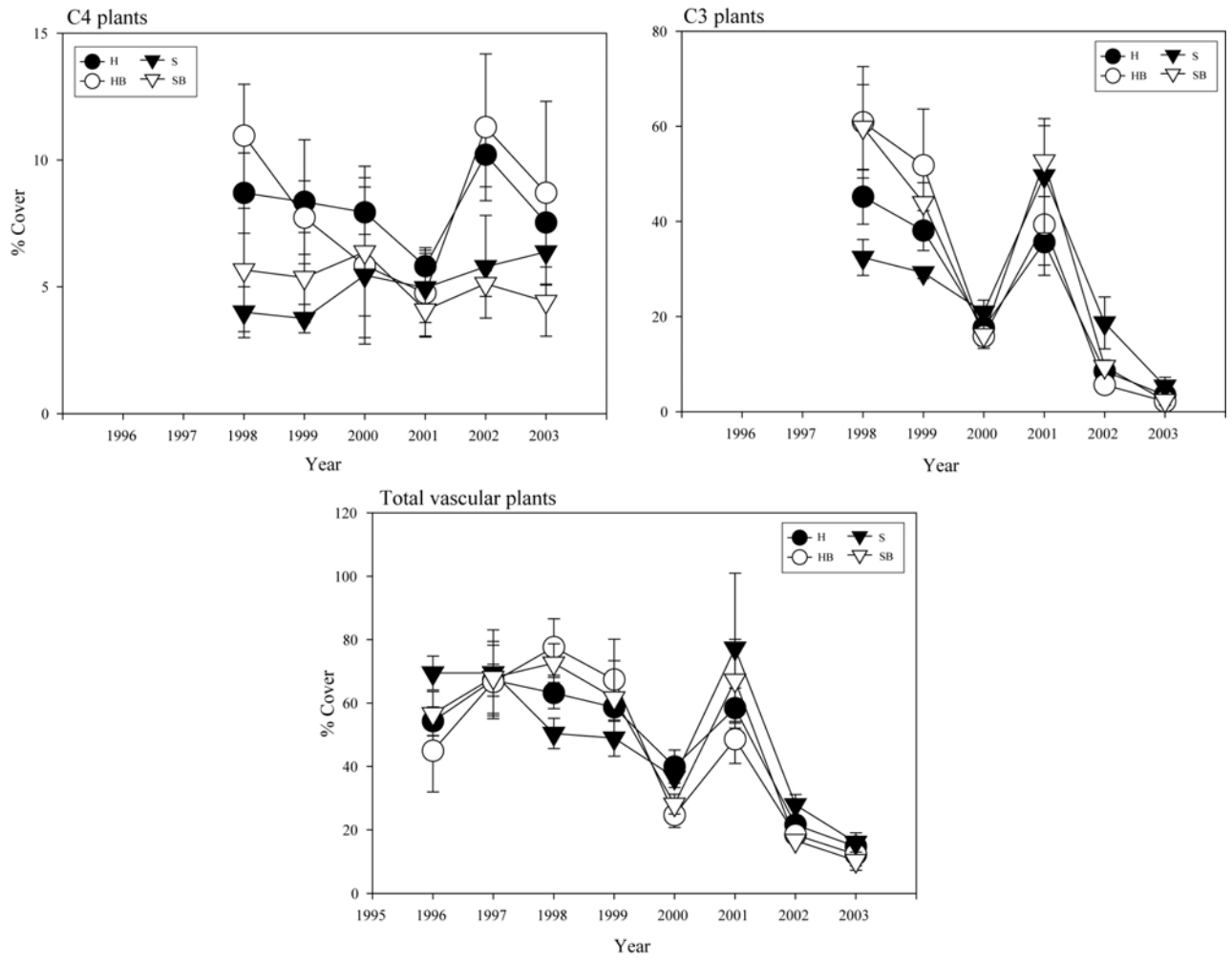


Figure 6. Cover of C_3, C_4 and total vascular plants during 1996-2003.

Effects of *Bromus* on Soil Phosphorus

Introduction

Soil phosphorus (P) availability is a key component of ecosystem productivity and sustainability. Aridlands ecosystems often have large amounts of total soil phosphorus, however labile (plant-available) soil P may vary by landscape position and/or by parent material. Under some circumstances soil P may limit productivity or co-limit productivity along with soil nitrogen availability in arid systems.

Interestingly, invasive plant species cause variation in soil nutrient availability. These changes have been measured best where invasive species are long-lived (trees) or where soils are changed so much that other species cannot grow eg: salinity. In western US arid land ecosystems, invasion by *Bromus tectorum* (hereafter referred to as *Bromus*) is pervasive in many areas and this species many dominate both cover and biomass after becoming established. For this reason it is a likely candidate species to examine effects on soil nutrients.

Finally, soil N nutrient availability is known to changes seasonally with large fluctuations during and after the growing season. Measurements of seasonal fluctuation soil P availability have not been made previously, although it is likely that such changes do ocurr. If soil P availability changes seasonally, it seems reasonable to expect that the invasive species may alter seasonal patterns.

Question 1. Does soil P availability change seasonally?
Question 2. Does soil P availability change in response to *Bromus* invasion?
Question 3. What soil P fractions and pools are most altered seasonally and in response to invasion?

Methods

To test for seasonal changes in soil P availability we designed three sampling regimes in the vicinity of Canyonlands National Park and one greenhouse study at the University of Denver. The first field study was conducted in 2002 at the Needles District in easily accessible terrain. This study is referred to as "SF monthly" and it is designed to test for monthly variation is soil phosphorus in three contrasting soils. The second field study was developed at a site in the Needles District as well. Abundant precipitation associated with El Niño conditions in 1994-1995 facilitated *Bromus* invasion of undisturbed desert grassland in a secluded area known as Viginia Park. Native bunchgrass species have persisted but diminished since the initial invasion, and our experimental design took advantage of this pattern where we tested for the effect of *Bromus* invasion on soil P. We refer to this study as "VP seasonal". The third field study was located near Moab, Utah at an easily reached site. We sampled soils to 60 cm depth at this site hence the study name "Deep soil P". Finally the greenhouse study at the University of Denver used four contrasting soils and tested for changes in soil P before and after *Bromus* under controlled ambient conditions.

For each of the studies soil samples were analyzed for soil P using a modified Hedley P fractionation method (Hedley et al. 1982; Cross and Schlesinger 1995). The method employs a sequential fractionation of soil P from 1 g of soil. The soil was not air dried before fractionation and was adjusted for by soil moisture content. The Hedley method separates soil P into fractions that may be combined into pools of soil phosphorus. These pools include labile P (plant-

available), non-labile P (non-plant-available), biochemical P (organic forms of P), geochemical P (inorganic forms of P), and total P (Cross and Schlesinger 1995).

Resin extractable inorganic P (Pi) is extracted with Dynambio brand anion exchange resin membranes. 0.5 M sodium bicarbonate ($NaHCO_3$) extracts readily solubilized-Pi and mineralized labile organic P (Po), readily mineralized from biomolecules available in the soil. When added together these three P fractions, resin-extracted Pi, $NaHCO_3$-Pi, and $NaHCO_3$-Po, form the labile P pool, and represents soil P that is readily available for plant use.

0.1 M sodium hydroxide (NaOH) extracts soil P fractions that labile moderately labile. These NaOH Pi and Po fractions are immobilized within microbes, stabilized as soil organic matter (SOM), or chemically attracted to iron (Fe) and aluminum (Al) dominated clay surfaces.

1 M hydrochloric acid (HCl) extracts Pi that is mineral bound in highly calcareous soils or occluded within alumina or hematite sesquioxides. This fraction is considered stable and is sometimes referred to as acid extractable P.

0.1 M NaOH sonication releases stabilized or residual, non-labile Pi and Po forms occluded in secondary compounds, primarily Fe and Al chelates. Taken together these fractions are referred to as sonicated P.

The occluded P remaining in the soil pellet cannot be distinguished between organic and inorganic forms. Therefore, the residual P remaining in the soil pellet is extracted as total residual P. The pellet is oven dried at 60°C for 24 hrs, ground by mortar and pestle, and 0.15 g is extracted for total residual P by NaOH fusion (Smith and Bain 1982). This fraction represents the most stabile form of P and the least plant-available P. Total P fractions are determined for $NaHCO_3$, NaOH, and sonication extracts by acidified 2.2 M ammonium persulfate ($(NH_4)_2S_2O_8$) digestion. Inorganic P is determined from these fractions by direct acidification with 0.90 M H_2SO_4. Organic P is calculated by the difference of Pi from total P. All samples were diluted and neutralized to match the carrying matrix of the auto-analyzer, then analyzed colorimetrically by flow injection according to the Lachat Instruments QuikChem Methods 10-115-01-1-A (2000) and 10-115-01-1-B (1998). Two Lachat methods were used in P determination dependent on the detectable levels of orthophosphates in each fraction (0-200 ppb P or 10-2000 ppb P).

By combining various combinations of fractions into soil P pools, we can observe biologically interesting trends in soil P (Cross and Schlesinger 1995). Labile P includes P extracted by resin-Pi, $NaHCO_3$-Pi, and $NaHCO_3$-Po. This pool represents readily solubilized, plant-available P. A second poll called biological P consists of the three organic P fractions; $NaHCO_3$-Po, NaOH-Po, and NaOH-Sonication-Po, and represents P forms that originated from biologically mineralized or immobilized compounds. Geochemical P consists of the inorganic P fractions; resin-Pi, $NaHCO_3$-Pi, NaOH-Pi, HCl-Pi, and NaOH-Sonication-Pi and is indicative of the P that is minerally bound to inorganic elements (Fe, Al, or Ca) or occluded within more complex, secondary compounds.

SF Monthly

The sampling design for this study used 4 randomly chosen permanent sample points at two locations called squaw flat and Indian creek (2 permanent points per location). After defining a 10 meter sample area (circular) around each sample point, composite samples from each of the 4 permanent sample sites were collected at monthly intervals. The composite samples came from 0-10 cm depth and each of the 10 composite sample consisted of 5 replicate samples from a 10 meter sample area. For each replicate five subsamples were composited into a single sample for that sample area from that date. Total samples per sample date: 4 permanent

plots x 5 composited replicates at 1 depth = 20 soil samples per month for each month in 2002. For these samples we used a partial Hedley fractionation procedure, where we measured P fractions up to and including the HCl fraction. Soils at squaw flat and at Indian creek are classified as Begay series soils which are coarse-loamy mixed, mesic Ustollic Camborthids.

VP Seaonal

The sampling design for this study used 4 types of plots selected because of their grass composition. We worked with soils where *Hilaria jamesii* and *Stipa orizopsis* persisted alone and in other areas where each species grew with *Bromus*. We sampled surface soils seasonally in 2002 and 2003. Because Viginia Park (VP) is difficult to access, sampling was limited to seasonal collections. At VP we collected composite samples (described above) in three replicates per site: one composite sample from each of 3 *H. jamesii* /no *B. tectorum* plots, one composite sample from each of 3 *H. jamesii* /*B. tectorum* plots, one composite sample from each of 3 *S. oryzopsis* /no *B. tectorum* plots, and one composite sample from each of 3 *S. oryzopsis* / *B. tectorum* plots. This resulted in a total of 12 composite samples total x 4 plots x 4 times a year. Soils at Virginia Park are classified as Begay series soils which are coarse-loamy mixed, mesic Ustollic Camborthids.

Greenhouse

The greenhouse study uses four soils from the Mojave Desert. The four soils vary in sand and $CaCO_3$ such that one soil has high sand and low $CaCO_3$, one has high sand content and high CaCO3, the third soil has low sand and low $CaCO_3$ while the fourth soil has low and high CaCO3. *Bromus* plants were grown for 100 d in the greenhouse in growth tubes using a completely randomized block design using a deliberately high density of plants (equivalent to ~2,800 plants/m^2). After biomass harvest the soils were analyzed for soil P fractions using a modified Hedley P fractionation procedure (described above).

Results

SF Monthly

Resin extractable P from the sites at squaw flats (SF) and Indian creek (IC) varies seasonally during the 12 month period from January through December 2002 (Figure 1.). Peaks in labile P occur in January and June at IC when resin extractable P more than doubles. Resin extractable P increases in June and in October at SF, with the greatest resin extractable P for all months at both sites recorded from samples taken in June at SF.

Labile phosphorus (also known as plant-available phosphorus) varies seasonally as well, with both sites following the same seasonal patterns (Figure 2). In general, the labile P pool is at an annual low in February and at an annual high in June. HCl extractable P varied monthly with a large spike in June for both sites (Figure 3). Lowest HCl extractable P occurred in January and February at SF and in February only for IC. January, June, July, September and December had the largest variability in measured HCl extractable P.

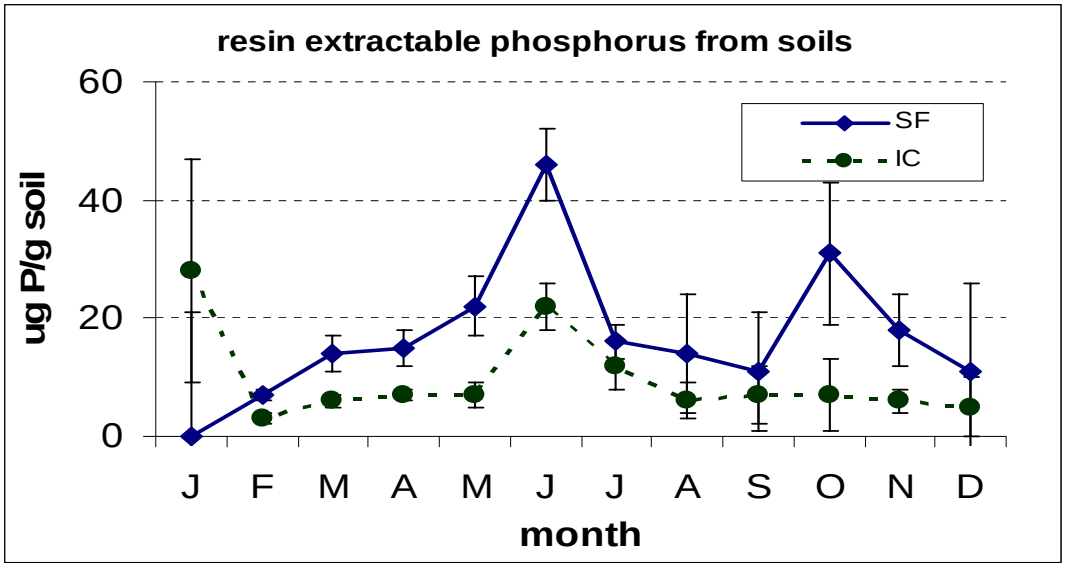


Figure 1. Resin extractable phosphorus from 0-10 cm soil depth at squaw flat (SF) and at Indian creek (IC). Values are averages +/- 1 standard deviation.

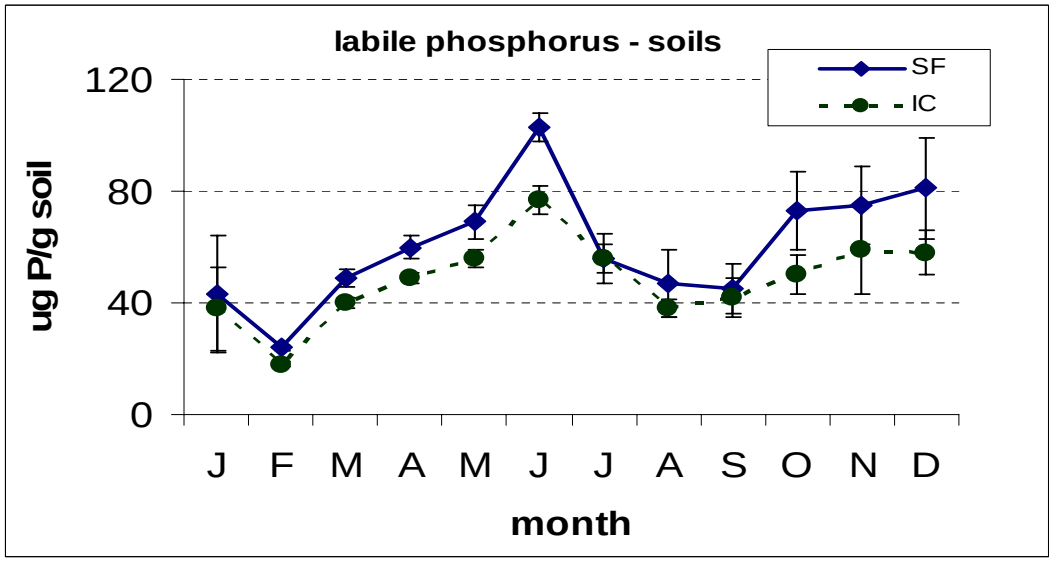


Figure 2. Labile phosphorus from 0-10 cm depth soils at squaw flat (SF) and at Indian creek (IC). Labile P is a phosphorus pool consisting of the sum of resin P, bicarbonate Pi and bicarbonate Po. Values are averages +/- 1 standard deviation.

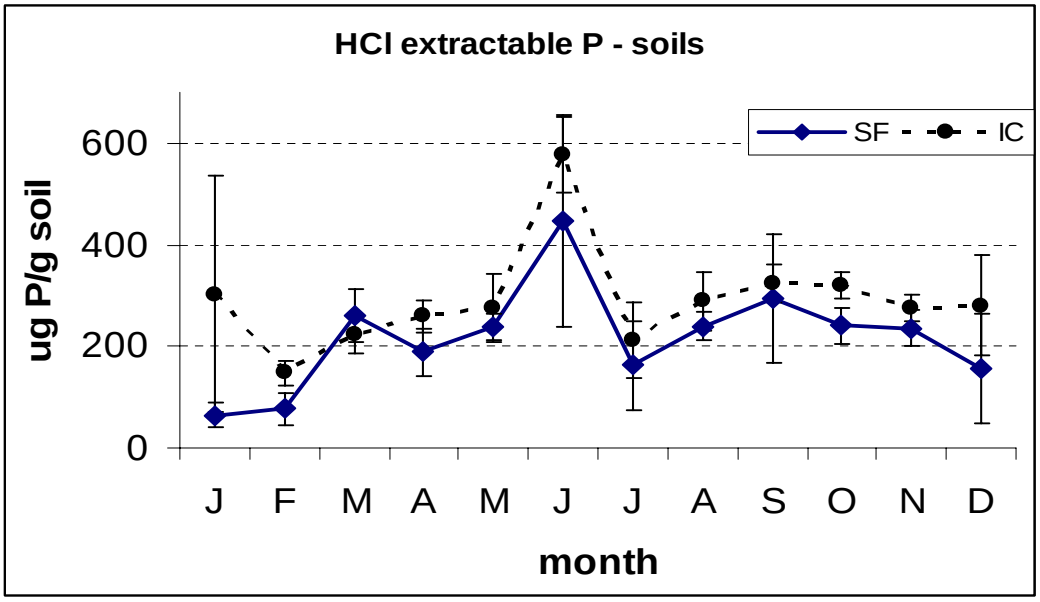


Figure 3. Monthly averages (+/- 1 standard deviation) for hydrochloric acid extractable P from 0-10 cm deep soils at squaw flat (SF) and at Indian creek (IC).

VP Seaonal

Labile soil phosphorus varies seasonally in soils at Virginia Park (Figure 4). The patterns of seasonality is similar for the two years in that labile peaks in early winter and then drops off in late spring. The pattern is dissimilar in that labile P never recovers (increases) in autumn of 2003.

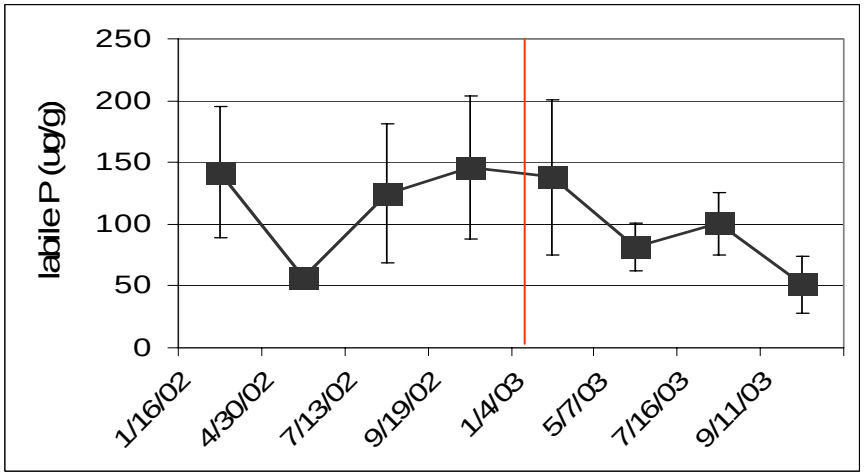


Figure 4. Seasonal averages (+/- 1 standard deviation) of labile soil phosphorus for all sites sampled in Virginia Park at 0-10 cm depth from 2002 and 2003.

To test for individual species effects and for the effect of *B. tectorum*, labile P measurements are sorted by sample site. Seasonality of labile P at sites where *B. tectorum* has

not invaded is very weak it the sites dominted by the native perennial grass *Hilaria jamesii* (Figure 5). A large drop in plant-available P occurs from winter to late spring in 2002, but the picture is less clear after that. In contrast to *H. jamesii*, labile P varies considerably from season to season in 2002 for a different native perennial grass *Stipa hymenoides* (Figure 6). From a low of 54 ug P/g soil in the late spring to a 2-year high of 138 ug P/ g soil in the autumn. Similar to the pooled samples and to H. jamesii, the pattern does not hold for seasons in 2003. Invasion by *Bromus* causes substantial changes to labile P at sites where native grasses persist to form an invasive x native grass mix.

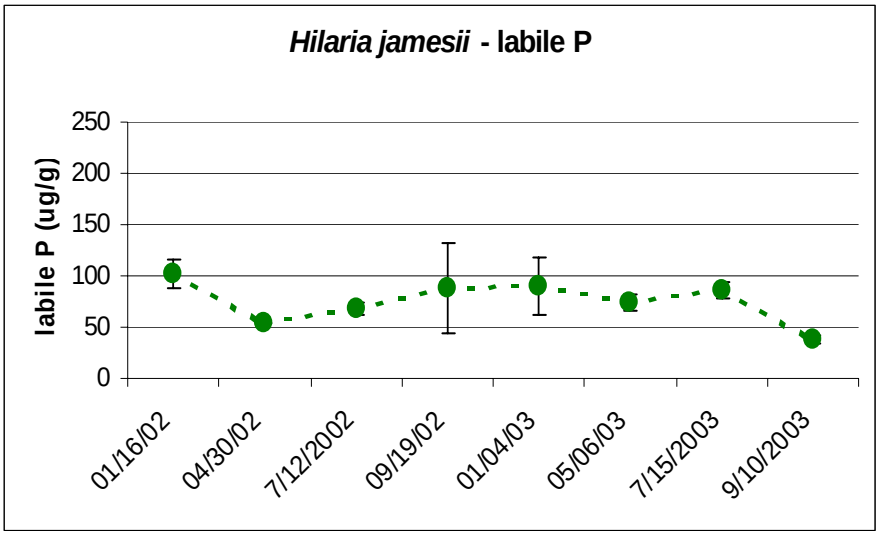


Figure 5. Seasonal measurements (average +/- 1 standard deviation) of labile soil phosphorus at Virginia Park. Soil samples are from 0-10 cm depth in areas that are dominated by *Hilaria jamesii* and that have not yet been invaded by *Bromus tectorum*.

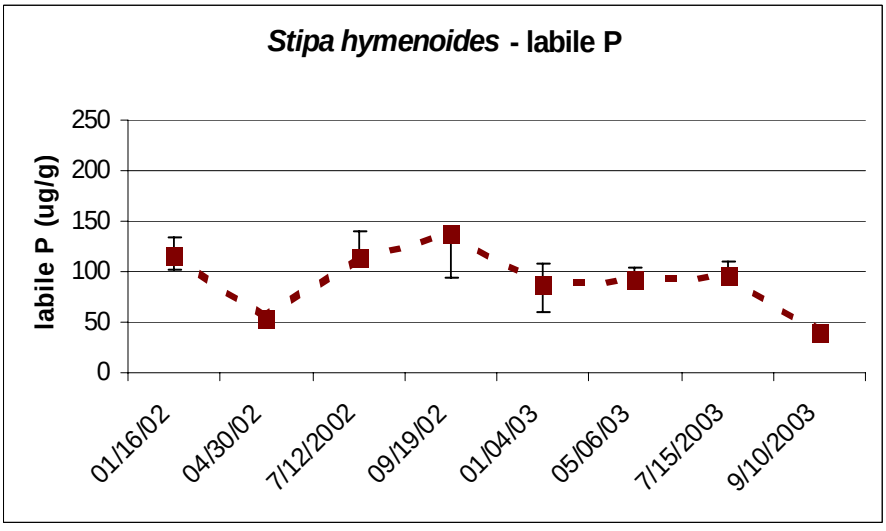
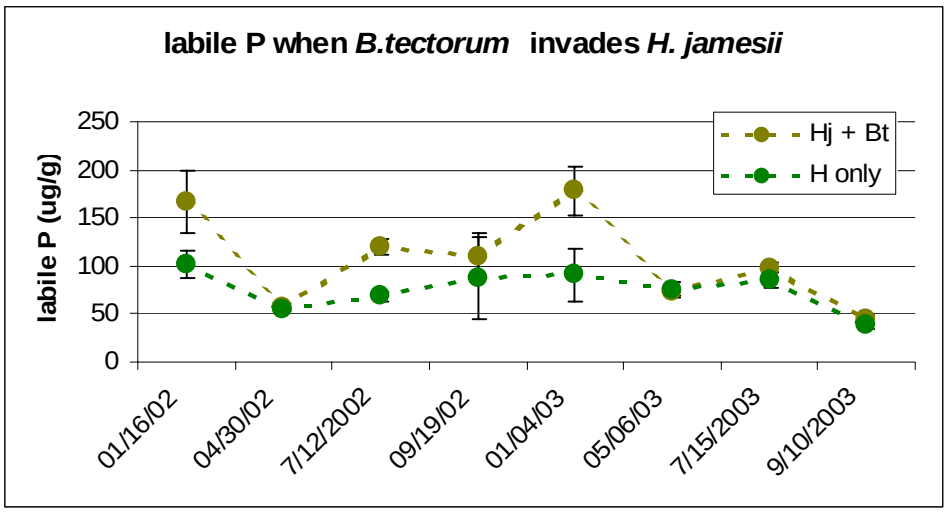


Figure 6. Seasonal measurements (average +/- 1 standard deviation) of labile soil phosphorus at Virginia Park. Soil samples are from 0-10 cm depth in areas that are dominated by *Stipa hymenoides* and that have not yet been invaded by *Bromus tectorum*.

a)



b)

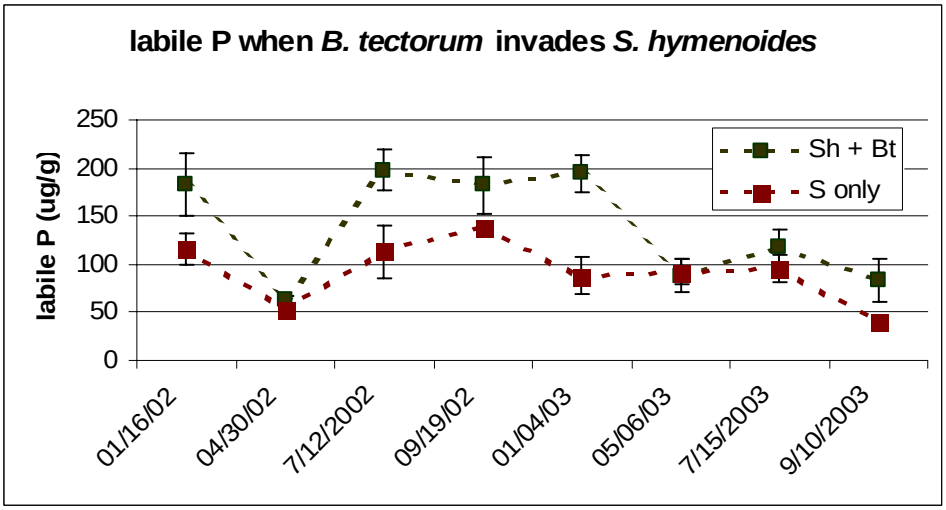


Figure 7. Labile soil phosphorus pool (average +/- 1 standard deviation) for sites where native perennial grasses a) *Hilaria jamesii* and b) *Stipa hymenoides* have been invaded by *Bromus tectorum*. Soils are from 0-10 cm depth.

Labile P increase substantially in the winter in soils where *H. jamesii* has been invaded by *B. tectorum* (Figure 7a), but except for mid summer 2002, there appear to be only minor increases in labile P. The pattern is quite different for labile P in soils where *S. hymenoides* is invaded by *Bromus* (Figure 7b). Firstly, labile P is increased in most seasons in both years. Secondly, labile P is increased by a larger amount than for *H. jamesii* x *B. tectorum* mixes. Labile P approaches 200 ug P/ g soil four times in the *S. hymenoides* plots.

Greenhouse study

Contrasting soils from the Mojave desert were used to grow *Bromus* under controlled conditions in the greenhouse at the University of Denver. The original design

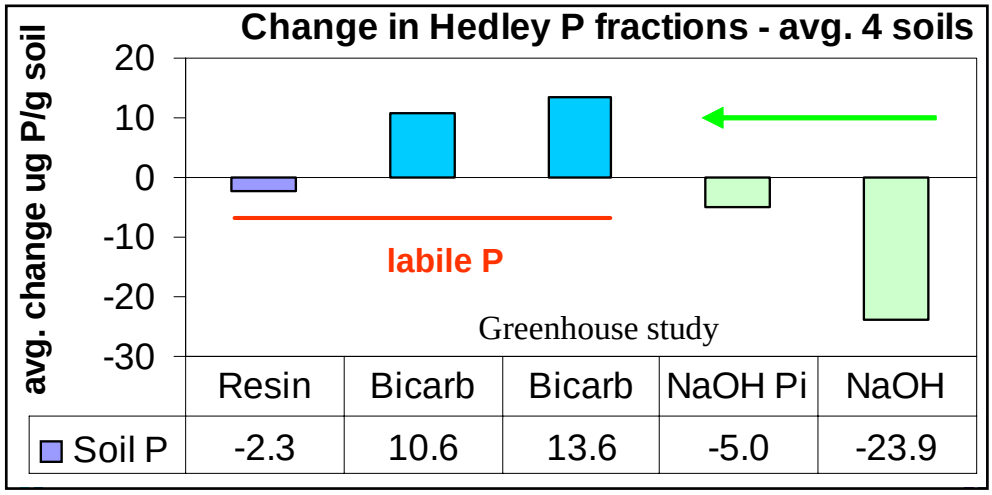


Figure 8. Change in soil P fractions for four Mojave soils (averages).

called for comparisons of the effects of *Bromus* on soil P in soils that very in sand and CaCo3 content. We did use the four soils for this experiment (as described in the methods section) however the changes in soil P fractions were so large and so unexpected that we pool the soils to convey this part of the results. The first analysis of soil P fractions that are plant-available (labile P) or that have been shown to be modified by heat, show that the NaOH P fractions are reduced and that the labile P pool is increased by nearly equivalent amounts (Figure 8). If we had stopped at this point, which is logical given most previous work, we would have missed the biggest part of the change in soil P.

Surprisingly, we found that the HCl extractable P pool decreased by an average of > 90% (Figure 9) which is similar to the % decrease of the NaOH fractions. However, because the HCl fraction is much larger than the NaOH, the absolute decrease is enormous in comparison to the NaOH fractions (Figure 10). This pattern hold for each of the four soils tested (Figure 11).

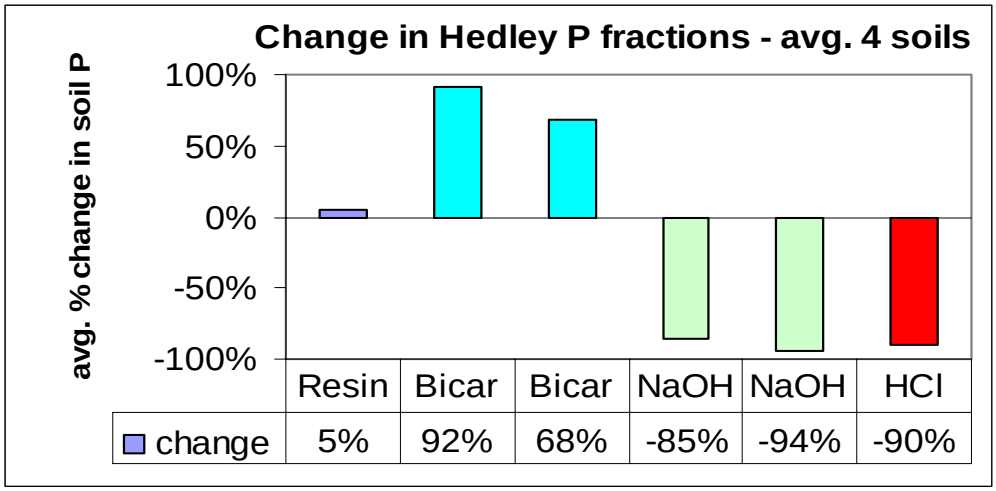


Figure 9. % change in soil P fraction for four Mojave soil (average).

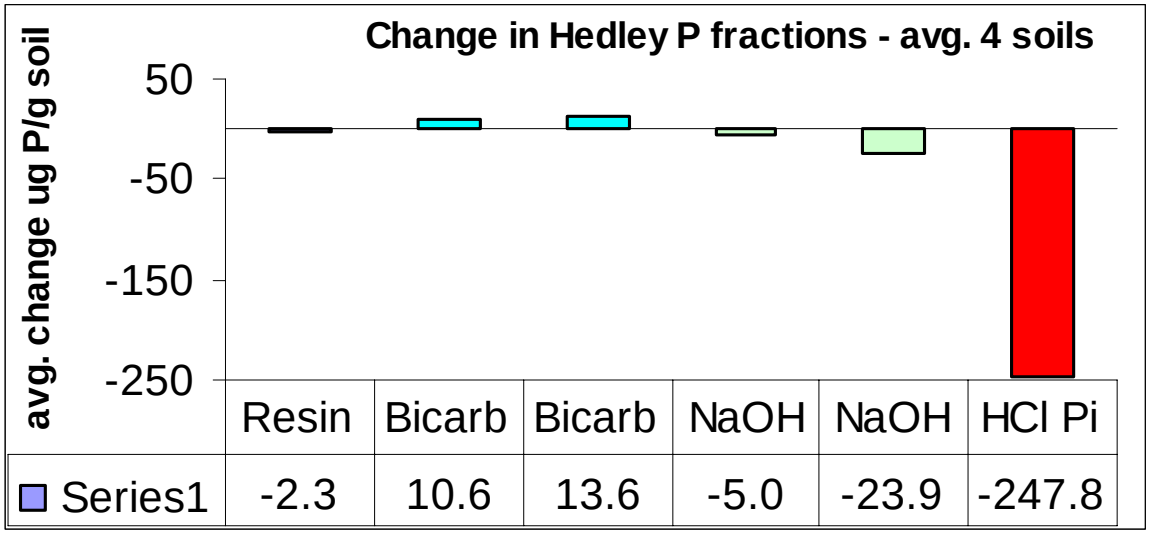


Figure 10. Changes in soil P fractions for four Mojave soils (averages).

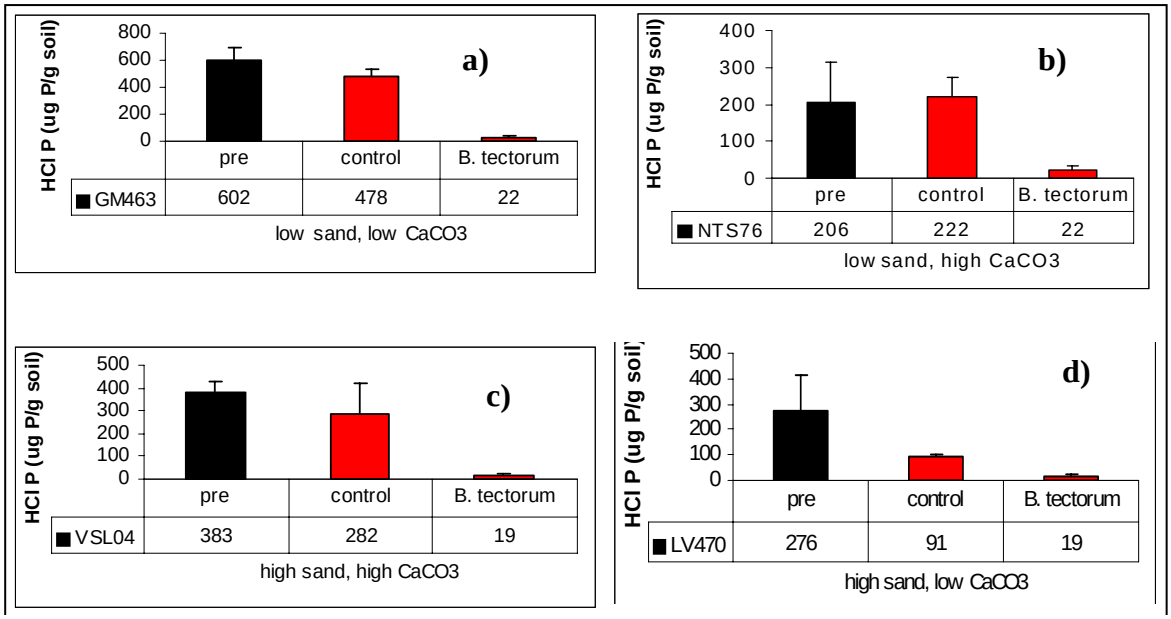


Figure 11. Changes in HCl extractable P for each of the four Mojave soils. Pre measurements are from soils before being planted with *Bromus*. Control measurements are from soils that had water added, but that were not planted with *Bromus*. B. tectorum is from for soils that had *Bromus* gwowing in them for 100 days. Bars are averages with 1 standard deviation shown. The soils were selected based on their sand and CaCO3 content (a-d).

Discussion

Monthly and seasonal changes in soil phosphorus fractions and pools are not known for wildland soils. We show substantial monthly changes in resin and labile phosphorus at two sites (SF and IC) in and near Canyonlands N.P. At SF, grazing ceased approximately 30 years ago however *Bromus* persists, and it certainly dominates the sites that we sampled. At IC, (which is

located outside the park boundary) *Bromus* is also present but is less abundant, as is all vegetation, due to grazing pressure. Pulses in soil nitrogen have been long known, yet pulses in soil P are not known widely. For both sites that changes in plant-available P are large enough that they should have an effect on soil microbes, and vascular plants. Because labile P is a pool (made up of three fractions), it is interesting to note that resin P (fig. 1) makes up approximately half of labile P, and that monthly trends for the two are quite similar. Of particular interest are the large pulses in resin P (Figure 1) and labile P (Figure 2) in the summer months that coincide directly with the die-back of *Bromus*. From this set of observations it is not possible to determine if *Bromus* causes the P pulse. In addition to plant available soil P changes, there are enormous monthly changes in HCl extractable P (Figure 3). This P fraction is known as occluded P (Walker and Syers 1976), calcium phosphate bound P (Hedley et al. 1982), and as stable Ca-bound P (Wager et al. 1986) hence it is a fraction that is expected to vary minimally from month to month. This is important in that this fraction makes up 30-40% of total P in these soils and is a likely contributor to both the labile P pool and even the resin P fraction.

From the soils sampled at Virginia Park it is also clear that there is a seasonal trend in plant available P (Figure 4), but the really interesting aspect of the VP data is shown when soils P fractions are considered in relation to native versus *Bromus* sites. The soils under one native grass (*H. jamesii*) shows moderate seasonal cycling of the labile P pool (Figure 5), while the other native grass (*S. oryzopsis*) show a mode accentuated pattern for the same soil P pool. Striking changes occur at sites where *Bromus* has become established (Figure 6) where labile P is increased in the surface soils for most seasons. The largest increases occur for the *S. oryzopsis* plots. The other change that occurs is the large drop in labile P in 2002 versus 2003. Biological activity was minimal in 2003 because of an intensive drought that persisted for most of the year. We suspect that this lack of moisture caused the decrease in labile P for the latter seasons in 2003.

Overall, the most surprising results from this study are derived from the experimental work in the DU greenhouse. To better understand how *Bromus* changes soil P, we grew *Bromus* in relatively high densities in desert soils for 100 days. Following analysis of soils prior to the treatment and following the treatment, we observed large changes in most soil P fractions, regardless of the soil properties. Our first observation was that the increase in the labile P pool coincides almost exactly with the decreases in both of the NaOH fractions (Pi and Po). The balance between the loss in NaOH P and the gain in the labile P pool is remarkable (Figure 8). After looking at other soil P fractions it became clear that another soil P fraction (HCl exatractable) also had large P losses (Figure 9). This is similar to the monthly changes that we observed from field observation (Figure 3). However, because HCl extractable P makes up such a large proportion of total P (approximately 30-40 %), the absolute amount of the losses is far in excess of the transfer out of the NaOH pool. What is even more remarkable is the consistency of this loss for all four of the soils tested. We have yet to resolve where this P fraction goes. In other words, the loss of so much of what has been considered “stable P” from the HCl extractable fraction matching gains in other P fractions creates a stoichiometric conundrum.

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Effects of Bromus on soil nitrogen and decompostion

Introduction

One of the most significant plant invasions in North America has been the establishment of *Bromus tectorum* L. (hereafter referred to as "*Bromus*") in arid regions of the intermountain West (Mack 1981, D'Antonio and Vitousek 1992). Invasive species threaten the stability of ecosystems worldwide by altering resource availability, trophic structure, and biodiversity (Vitousek 1992). Soil N is one of the most important components in maintaining ecosystem stability, and the introduction of non-native plants can alter N cycling through changes in litter quality and quantity (Evans et.al. 2001) and soil food webs (Belnap and Phillips 2001). The response of arid and semi-arid ecosystem nutrient availability to invasion is not known, largely because we have little understanding of C and N dynamics in these ecosystems.

Understanding of belowground carbon (C) and nitrogen (N) cycling is a key factor in predicting how ecosystems will respond to invasions. Cycling of carbon (C) and nitrogen (N) through soil microbes is fundamental to the stability of any ecosystem (Zak et al. 2000) and has significant effects on community structure, ecosystem-level fluxes of energy and nutrients, and regional-scale estimates of C storage. Soil C and N cycling is controlled by the input of plant litter and the diversity and metabolism of soil microbes (Zak et al. 1993, Pregitzer et al. 1995, Barrett and Burke 2000). Soil bacterial and fungal populations act as a pool of relatively labile C and N compared to soil organic matter (Stevenson and Cole 1999, Barrett and Burke 2000) and control amounts of biologically available N (amino acids, NH_4^+ and NO_3^-). The N mineralized from soil organic matter by soil microbial activity is available for uptake by plants and microbes. Therefore, increases in soil C availability have the potential to increase microbial activity (Zak et al. 1993, Groffman 1999, Zak et al. 2000, Billings et al. 2002), and microbial N cycling (Schimel et al. 1989, Davidson et al. 1990, Schaeffer et al. 2003) and can act as a feedback on plant growth through changes in N availability (Zak et al. 1993). However, in most ecosystems there exists a fundamental lack of knowledge about the organisms responsible for fluxes of energy and nutrients. In order to more fully understand soil C and N dynamics, there is a critical need to relate the sources of C substrate utilized by heterotrophic microorganisms to decomposer community composition.

The pattern of *Bromus* invasion is among the best understood of any invasive species (Mack 1981, Vitousek et al. 1997), yet relatively little is known about how invasion alters ecosystem C and N cycling. Bolton et al. (1993) found that mineralization potentials for *Bromus* stands were greater than native shrub communities in the shrub-steppe, but exhibited lower spatial heterogeneity than native shrub communities. Microbial biomass C and N and soil respiration were also greatest in *Bromus* stands (Bolton et al. 1993). Although *B. tectorum* is one of the most studied exotic plant species in recent years, separating the confounding effects of invasion and disturbance on ecosystem functions has been difficult because undisturbed communities are extremely rare (Rimer, 1998; Evans and Belnap, 1999; Belnap and Phillips, 2001; Evans et.al., 2001). An undisturbed arid grassland (Virginia Park) in southeastern Utah provides the opportunity to study the influence of *B. tectorum* invasion without physical disturbance. Initial surveys showed 0.4% *B. tectorum* cover in Virginia Park (Kleiner and Harper, 1977), until the spring of 1994 when approximately 25 small (<0.1 ha) distinct *B. tectorum* patches were found scattered throughout Virginia Park (Belnap and Phillips, 2001).

There have been two previous studies completed in this system looking at the effects of plant invasion on N dynamics. Rimer (1998) performed a study investigating the initial effects of invasion by *Bromus* on disturbed and pristine ecosystems. It was shown that only two years after invasion, *Bromus* was able to alter N dynamics in this system. Invasion by *Bromus* led to an increase in total soil N content at the soil surface, decreased the size of the labile N pool, and a decrease in net mineralization rates. Rimer (1998) hypothesized that these changes resulted from *Bromus* litterfall. Evans et al. (2001) performed a study in this same site looking at how invasion of *Bromus* into two communities of native perennial grasses (*Stipa hymenoides* and *Hilaria jamesii*) has altered N dynamics. Mean litter fall in invaded communities was 125% greater than non-invaded communities, and *Bromus* litter had a significantly lower total N, higher C:N, and lignin:N ratios than natives. Net mineralization was 50% lower in invaded soils, which also caused an increase in the immobilization index (C mineralized per unit N mineralized) of invaded soils. Evans et al. concluded that invasion by *Bromus* leads to a series of positive feedbacks that result in decreased nitrogen availability and alterations to species composition. Two important points from these studies are 1) that there have been significant alterations to the N cycle with invasion by *Bromus*, and 2) that these changes occurred as short as 2 years after *Bromus* establishment. The exact mechanisms behind these findings are not known.

Our goal for this project was to determine the mechanisms that explain how *Bromus tectorum* invasion has significantly altered soil N cycling processes in native arid grassland communities. We hypothesized that changes in the composition of soil organic matter from *Bromus* litter inputs have altered the functional composition of the soil microbial community. To that end, we combined monitoring of plant-available N and plant and soil isotopic composition (Rimer 1998, Evans et al. 2001) with measurements of C and N fluxes, microbial community composition, and microbial substrate utilization from laboratory soil incubation.

Materials and Methods

The study site was located in Virginia Park (38º05’43” N, 109º50’31” W) within the Needles District of Canyonlands National Park, Utah, USA. Annual precipitation is 214 mm (Western Regional Climate Center, Reno, Nevada, USA). Virginia Park is a 97 ha arid grassland that has been protected from grazing by high rock walls (Kleiner and Harper 1972). Vegetative structure of this system is composed of the native perennial bunchgrasses *Stipa comata* (Trin. and Rupr), *Stipa hymenoides* (R & S), and *Hilaria jamesii* (Torr.) Benth. Soil interspaces are covered with biological soil crust consisting of moss, lichens, and cyanobacteria (Kleiner and Harper 1972). The N_2-fixing lichen and cyanobacteria components of the crust are the dominant sources of N in this ecosystem (Evans and Belnap 1999). Soils are part of the Begay series and are classified as coarse-loamy, mixed, mesic Ustollic Camborthids (Kleiner and Harper 1972). *Bromus* has existed in Utah since the late 1800’s (Mack 1981), however it was not a conspicuous member of the grassland communities in Virginia Park (Kleiner and Harper 1972, 1977) until 1994 when it became dominant in many stands after a mild winter (Belnap pers. comm.). We identified invaded and non-invaded stands of two community types within Virginia Park for more intensive study of the short-term (years) changes that occur in soil C and N cycling in undisturbed grassland ecosystems. The two community types being invaded by *Bromus* (C_3 annual) were dominated by either *Hilaria jamesii* (C_4 perennial) or *Stipa hymenoides* (C_3 perennial). Three 30 X 20 m plots were established in both invaded and non-invaded stands of each community (12 total) during May 1996.

Experimental Design

Plant-available nitrogen

Cation-anion exchange resin (10 g) (Dowex MR-3, Dow Chemical) was placed in nylon pouches (Binkley and Matson 1983, Binkley 1984) in the top 5 cm of the soil surface. Bags were replaced approximately every eight weeks from September 2000 through December 2003. Upon removal, bags were transported to the laboratory for analysis. Each bag was extracted in 50 ml 2M KCl, and extracts were analyzed for NH_4^+ and NO_3^- concentrations using an autoanalyzer (Alpkem FS3000, OI Analytical, College Station, TX).

Soil and plant stable isotopes

Foliage from the three grass species (*Bromus tectorum*, *Stipa hymenoides*, and *Hilaria jamesii*) were sampled in 2001 in Virginia Park, Chesler Park, and Squaw Flat. Vegetation samples were oven-dried for 48 h at 60°C and ground to a fine powder for analysis. Soils were sampled from the top 1 m of the soil horizon. Soils were passed through a 2 mm sieve and pooled according to site, native plant species, and invasion status. Soil samples were then air dried, ground to a fine powder, and acid washed three times with 3N H_3PO_4 to remove carbonates. Both vegetation and soil samples were analyzed for %N, %C, $\delta^{13}C$ and $\delta^{15}N$ on a Carlo Erba elemental analyzer (NA1500 CHN Combustion Analyzer, Carlo Erba Strumentazione, Milan) coupled to a Finnigan Delta$^+$ mass spectrometer (Finnigan MAT, Bremen, Germany) via a Finnigan Conflo II Interface.

Long-term incubation: cumulative N, C, and N_2O-N mineralization

Soils were collected following the sampling protocol described for soil isotope data. Fifty grams of each soil type was placed in 5.3 cm diameter x 5.0 cm tall polyvinyl chloride cores, held by glass fiber filter paper taped to the bottom. We vacuum extracted inorganic N from each soil sample with N-free nutrient solution (Nadelhoffer 1990) at the beginning of the incubation and placed each soil sample in a 1 L gas tight jar equipped with a gas sampling port. Samples rested on glass marbles in the jar bottoms to allow air flow across the bottom of the cores. On days 7, 19, 42, 84, 228, 315, and 385 we extracted 9 ml of gas sample from each jar. Gas samples were stored in pre-evacuated, gas tight vials. After gas sampling, we vacuum extracted inorganic N from each soil sample with N-free nutrient solution, placed the samples back in the jars, and took another gas sample before sealing the jars. Between sampling dates, samples were stored in the dark at 30°C. Extracts were analyzed colorimetrically for ammonium (NH_4^+) and nitrate (NO_3^-) on an autoanalyzer. Net N mineralization was calculated as the difference in soils' inorganic N content between extraction dates. Gas samples were analyzed for CO_2 and N_2O on a Shimadzu 14A gas chromatograph (Dallas, USA) equipped with thermal conductivity (CO_2) and electron capture (N_2O) detectors. Rates of C and N_2O evolution were calculated as the CO_2 concentration and N_2O increase over time respectively, accounting for jar headspace and soil weight.

We applied an exponential model to net N mineralization relative to total soil N (Bonde and Rosswall 1987, Wedin and Pastor 1993) to estimate pool sizes of labile N, rate constants for mineralization of labile pools, and mineralization rates of recalcitrant pools:

$$N_t = N_l(1 - e^{-h_l t}) + c_r t$$

where N_t is the amount of N mineralized at time t, N_l is the pool size of the labile pool of N relative to total soil N, h_l is the rate constant for the labile N pool, and c_r is the mineralization

rate of the recalcitrant pool of N. The model assumes that mineralization of recalcitrant N is constant and does not decrease over time. We estimated parameter values using a non-linear curve fitting procedure (PROC NLIN, SAS 8.01) on net N mineralization data. This procedure finds the best fitting equation by minimizing the sum of squares of the residuals. We tested the robustness of parameter estimates by changing the starting values of the iterative procedure to values within the 95% confidence intervals; no change in parameter estimates resulted.

Long-term incubation: microbial biomass, organic N, respired $\delta^{13}C$, and PLFAs

A second set of samples were incubated for destructive sampling of microbial biomass N, organic N, and phospholipid fatty acid (PLFA) analyses. Soils were collected and incubated in the same manner as previously described with the only difference being that 250 g of soil was incubated in 5 acetate tubes (2.5 cm diameter by 10 cm long) with glass fiber filter paper taped across the bottom. For each of the 12 plots, four replicates were incubated and one replicate randomly chosen for destructive sampling on a given date. This same suite of measurements was also conducted on dry soils (day 0) prior to the start of the experiment. Of the 250 g of soil, 16 g was used for microbial biomass and organic N, 6 g for soil moisture content, 50 g for PLFA analysis, the remaining soil was withheld for soil isotopic content and gross N flux analysis (which did not occur except on dry soils prior to incubation).

Microbial biomass N was estimated on days 1, 27, 168, and 388 of the incubation using the chloroform ($CHCl_3$) fumigation extraction technique outlined by Brookes et al. (1985) and used by Gallardo and Schlesinger (1992) in a Chihuahuan Desert ecosystem. Two 8 g aliquots of soil were placed in separate 50 ml centrifuge tubes. One tube was immediately extracted in 40 ml 0.5M K_2SO_4 for 24 h. The extracts were then filtered through filter paper (Whatman #4), and the extractant stored at 4 ºC. Total N in the extractant was digested to convert all organic N to NO_3^- using a persulfate digest (D'Elia et al. 1977). Nitrate concentrations were measured colorimetrically using the autoanalyzer. Two large cotton balls dosed with 3 ml of hydrocarbon-free $CHCl_3$ were inserted into the headspace of the second tube then incubated for 5 d at 30 ºC before extraction. The difference between fumigated and unfumigated sub-samples, when divided by the extraction efficiency (K_n) gives the microbial biomass N. Microbial biomass for the samples was calculated using a K_n of 0.69 (Brookes et al. 1985, Gallardo and Schlesinger 1992). The extractable organic N was defined as that fraction of the organic N pool that is soluble in 0.5M K_2SO_4. Unfumigated microbial biomass N samples were used to estimate this parameter.

On days 1, 12, 28, 35, 43, 64, 242, 316, and 388 a random replicate was sampled for $\delta^{13}C$ of headspace CO_2. Soil respired $\delta^{13}CO_2$ was estimated by collecting 20 to 100 µl of headspace air in a gastight syringe (Vici Precision Sampling, Baton Rouge, Louisiana) and injecting the air into a mass spectrometer (Finnigan MAT, Bremen, Germany) with a trace gas condensing device (Precon, Finnigan MAT) used to separate CO_2 from N_2O in air samples.

Determining the isotopic composition of bacteria and fungi in natural samples is difficult since microbial biomass cannot be separated from other organic material. The use of bacterial and fungal phospholipid fatty acids (PLFA) as isotopic biomarkers is advantageous because they include several compounds unique to bacteria or fungi, rapidly turn over when the organism dies, and thus are only associated with recently formed and living biomass (Parkes 1987, Tunlid and White 1992). The isotopic composition of PLFAs has been related to biosynthetic pathways (Teece et al. 1998), and specific substrates (Abraham et al. 1998) and documents bacterial nutrition. Therefore the isotopic composition of PLFAs represents a potentially powerful tool for

delineating substrate source of natural assemblages of bacteria (Abraham et al. 1998, Boschker et al. 1999) and fungi (Phillips et al. 2002).

Total lipids were extracted from 50 g of dry soil and from 50 g sub-samples on day 27 of the incubation using a modified Bligh-Dyer procedure (Bligh and Dyer 1959, Fredrickson et al. 1986). An aminopropyl ion exchange column was used to separate the neutral lipids, free fatty acids, and phospholipids from one another in each sample following lipid extraction (Agren et al. 1992). Following acidification, fatty acids in the phospholipid fraction were converted to their corresponding fatty acid methyl esters (FAMES) using BF_3 in methanol. Each FAME was quantified and identified using GCMS with a 70% cyanopropyl polysilphenylene-siloxane column (BPX-70, 50m) and known standards. Isotopic composition of individual fatty acids were determined using an HP6890 GC coupled to a Finnigan Delta$^+$ via a Finnigan GC/CIII combustion interface. The same GC column, oven and injector conditions used for GCMS analysis were employed in the isotopic analysis of the FAMEs. A correction for the addition of the methyl carbon from BF_3/methanol derivatization was calculated for each fatty acid by mass balance from the analysis of free and methylated standards (Abrajano et al. 1994).

Gross N fluxes

A modified version of the ^{15}N isotope pool dilution method as outlined by Hart et al. (1994) was used to measure gross flux rates. Five 50 g sub-samples of soil were used to measure each of the following: $^{15}NH_4^+$ at 0 h, $^{15}NO_3^-$ at 0 h, $^{15}NH_4^+$ at time 24 h, $^{15}NO_3^-$ at 24 h, and a control. Each subsample was placed in a plastic bag and labeled with excess ^{15}N 6ml injections with a syringe with the controls receiving water only. Samples designated as "time 24" samples were placed in an incubator (20ºC) for 24 hours to be extracted at the end of that time period in 100 ml of 2M KCL, resulting in a 2:1 soil to extractant ratio. Samples that are designated as "time 0" were extracted immediately. After addition of KCl, extracts were shaken for two hours and placed in a cold room (4ºC) overnight. The next day, extracts were filtered (Whatman #4) and colorimetrically analyzed on an autoanalyzer for NH_4^+ and NO_3^- concentration. Remaining N in extracts were transferred onto acidified quartz filter disks using the diffusion procedure as outlined in Hart et al. (1994) for stable isotope analyses. Gross rates were calculated from changes in the inorganic N concentrations and the changes in the atom percent excess of soils at 0 and 24 h.

Results and discussion

Previous studies of plant-available nitrogen in a recently invaded grassland (Virginia Park) observed a decrease in invaded plots at times of peak N availability (roughly July through September, Rimer 1998, Evans et al. 2001, and Sperry unpublished data). This pattern has reversed itself in 2002 with greater plant-available N in invaded plots of both *Stipa hymenoides* and *Hilaria jamesii* at times of peak N availability (Figures 1 and 2). The isotopic composition of leaves and soil is also similar to that from previous studies (Rimer 1998 and Sperry unpublished data). For the three sites along a gradient in the time since *Bromus* invasion (VP=Virginia Park < CP=Chesler Park < SF=Squaw Flat) there is an increase in leaf $\delta^{15}N$ for *Stipa*, *Hilaria*, and *Bromus* (Figure 3) suggesting changes in soil N cycling processes. The $\delta^{13}C$ of leaf material remains relatively constant within species across sites and invasion status (Figure 4). The $\delta^{13}C$ and soil organic C of soils from the top 10 cm in Virginia Park were not significantly altered by Bromus invasion (Table 1). Similarly the findings of Rimer (1998) invasion by Bromus has increased the total soil N in Stipa stands (Figure 5) and altered the

pattern of nitrogen stable isotope composition with depth. Plotting soil isotope composition versus nitrogen concentration provides a mechanism to track the pattern of invasion and possible assess the health of other invaded ecosystems (Figure 6). These results combined with existing observations that aboveground litter quantity and quality have changed with *Bromus* invasion (Evans et al. 2001) led us to hypothesize that litter inputs from invasive *Bromus tectorum* change the carbon and nitrogen substrate composition of soil organic matter leading to changes in the structure and function of the microbial community that in turn feed back into changes in ecosystem-level carbon and nitrogen cycling. To test this hypothesis we conducted a laboratory incubation in which we measured labile, recalcitrant, and microbial N pools and fluxes, as well as microbial community composition and C substrate utilization.

Pools of labile N, the amount of N, and N_2O-N mineralized over the course of the long-term incubation show that there are significant effects of *Bromus* invasion in *Stipa* soils (Figure 7, Table 2; also see appendix). Total C mineralized, labile rate constant, and recalcitrant N mineralization rate were not different either with invasion or between grassland communities. There was greater N_2O-N production from *Stipa* grasslands relative to *Hilaria* communities suggesting greater amounts or activity of nitrifier/denitrifier populations in these soils. In *Stipa* plots, there were significantly greater amounts of labile N (N_l) and N mineralized in invaded compared to non-invaded plots.

The amount of N in microbial biomass was not affected by invasion, but there were differences in the amount of labile organic N (Figure 8). Biomass N was not different with invasion or between *Hilaria* and *Stipa* communities, but organic N from non-fumigated K_2SO_4 extracts was greater in invaded compared to non-invaded *Stipa* communities.

Soil N cycling appeared to increase with *Bromus* invasion. Gross rates of NH_4^+ mineralization, immobilization, and NO_3^- nitrification were greater with invasion in both *Hilaria* and *Stipa* grasslands (Figure 9). It is interesting to note that net mineralization rates were not different between *Hilaria* plots, but were greater in invaded *Stipa* plots compared to non-invaded plots. This highlights the point that aspects of N dynamics can remain hidden when only net rates are measured.

Phospholipid fatty acids (PLFAs) of soil microbes were extracted from soil samples for determination of microbial community structure and substrate utilization patterns. The fatty acids extracted from Virginia Park soils can be used as biomarkers for specific classes of soil microorganisms: general microbial biomarkers (14:0, 16:0, 18:0, 18:1cis, 18:1trans, 20:0, and 22:0), gram$^+$ bacteria (terminal methyl branched i15:0, a15:0, and i16:0), gram$^-$ bacteria (cyclopropyl cy18:0 2-hexyl, cy18:0 2-octyl), fungal (polyunsaturated 18:3 and γ18:3), and actinomycete (mid-chain methyl branched 10me19:0). Given that the $\delta^{13}C$ of *Hilaria* and *Bromus* plant material differs greatly (Figure 4) and there is a relatively fast turnover time for PLFAs, the $\delta^{13}C$ of PLFA C should be reflective of recent C inputs into microbial biomass and the source of C input (*Hilaria* versus *Bromus* litter) may be determined. In addition these patterns in substrate utilization can be partitioned across the bacterial and fungal components of the soil microbial community. In dry soils (i.e. under field conditions), for the all the PLFAs measured, the only significant difference between native and invaded communities was found for a bacterial biomarker (a15:0) in *Hilaria* plots (Figure 8). After 27 days of incubation at constant temperature and moisture nearly all the biomarkers isolated in *Hilaria* plots show differences in substrate utilization with *Bromus* invasion (Figure 10). Fungal biomarkers disappear by this time while a biomarker for actinomycete biomass appears. There was no change in the $\delta^{13}C$ of

PLFAs between native and invaded *Stipa* plots with the exception of the actinomycete biomarker (10me19:0).

For the dry soils, the $\delta^{13}C$ for the bacterial biomarker (a15:0) was plotted with the $\delta^{13}C$ of the CO_2 respired from the soil microbial community during the first 24 h of incubation (Figure 11), the same 1.5 to 2.0 ‰ difference was observed for non-invaded versus invaded *Hilaria* plots. This suggests that the bulk of respiration in *Hilaria* soils is coming from bacterial populations that are preferentially utilizing *Bromus* organic material when it is available. This shift in substrate utilization in bacteria is accompanied by an increase in activity as measured by respiration in invaded compared to non-invaded *Hilaria* communities (Figure 12).

The structure of the soil microbial community also changes with invasion. The relative abundance of fungal biomarkers as measured by percent of total PLFA C (Figure 13) was lower in invaded *Hilaria* and *Stipa* grasslands while bacterial and general biomarkers were unaffected. Together these data suggest that *Bromus* invasion stimulates the activity of bacterial populations while adversely affecting the abundance of the fungal population in *Hilaria* communities. The decrease in fungal abundance may be due to a decrease in either the number or extent of mycorrhizal associations with *Hilaria* and *Stipa*.

In summary, the results of this experiment suggest that different processes are occurring in *Stipa* and *Hilaria* communities that are leading to the same effects as measured by plant-available N and stable isotopes. In *Stipa* communities there is an increase in the amount of labile soil organic N with *Bromus* invasion, coupled with an overall increase in microbial N cycling as measured by both gross and net rates of soil N transformations (mineralization, immobilization, and nitrification). For *Hilaria* communities there was no effect of *Bromus* invasion on labile soil N pools, but as with *Stipa* communities, overall N cycling rates were greater as measured by gross N fluxes. In addition differences in the stable isotopic composition ($\delta^{13}C$) of *Hilaria* (C_4) and *Bromus* (C_3) allow for the partitioning of microbial utilization between these two substrates. It was observed that *Bromus* invasion appears to stimulate the activity of at least a portion of the soil bacterial which preferentially decomposes *Bromus* litter rather than that from *Hilaria*. Analyses of soil microbial community structure also indicate that *Bromus* invasion significantly decreases the proportion of fungi in both native communities. These findings show that *Bromus* invasion can significantly alter the composition of the soil microbial community by changing the proportion of soil bacteria to fungi and increasing bacterial activity. These shifts in community structure and substrate utilization lead increased rates of soil N cycling that in turn affect the amounts of plant available N in these arid grassland ecosystems.

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Tables and Figures

	Hilaria		*Stipa*	
	Non-invaded	**invaded**	**Non-invaded**	**invaded**
$\delta^{13}C$	-19.7 (0.8)*a*	-20.1 (0.4)*a*	-22.0 (0.5)*a*	-20.9 (0.5)*a*
$\delta^{15}N$	3.5 (0.7)*a*	4.1 (0.5)*a*	3.5 (0.2)*a*	4.3 (0.3)*a*
SOC	4393 (215)*a*	4620 (328)*a*	3837 (158)*a*	4726 (437)*a*
total N	460 (21)*ab*	502 (39)*ac*	407 (16)*b*	526 (43)*c*
C:N	9.5 (0.1)*a*	9.2 (0.1)*ab*	9.4 (0.1)*ab*	9.0 (0.1)*b*

Table 1. Mean soil stable isotopic composition ($\delta^{13}C$ and $\delta^{15}N$, ‰), soil organic carbon (SOC, g C kg^{-1} soil), total N (g N kg^{-1} soil), and C:N from 0 to 10 cm depth in invaded and non-invaded stands of *Hilaria* and *Stipa* in Virginia Park, Canyonlands, 2002. Numbers in parentheses denote the standard error of the mean.). Lowercase letters (*a,b,c*) denote significant differences (P<0.05) between treatment means within a given parameter.

	Hilaria		*Stipa*	
	Non-invaded	**invaded**	**Non-invaded**	**invaded**
Total C mineralized	2.20 (0.21)*a*	2.22 (0.18)*a*	1.90 (0.04)*a*	2.30 (0.33)*a*
Total N_2O-N mineralized	0.13 (0.02)*a*	0.18 (0.06)*a*	0.35 (0.12)*b*	0.36 (0.10)*b*
Total N mineralized	60.73 (13.00)*ab*	83.17 (18.10)*a*	52.22 (3.87)*b*	91.99 (5.07)*c*
N_l	40.92 (11.75)*a*	41.01 (11.99)*a*	20.92 (6.96)*b*	45.73 (8.27)*a*
h_l	0.04 (0.03)*a*	0.04 (0.03)*a*	0.03 (0.02)*a*	0.04 (0.01)*a*
c_r	0.05 (0.04)*a*	0.10 (0.04)*a*	0.08 (0.02)*a*	0.12 (0.03)*a*

Table 2. Cumulative C, N_2O-N, and N mineralized as well as parameter estimates from exponential model applied to laboratory incubation data. Means and standard errors of C (mg g^{-1}), N_2O-N (µg g^{-1}), and N mineralized over 388 days are presented. Parameter estimates standard errors are: labile N pool (N_l, µg g^{-1}), the rate constant for the labile pool (h_l), and the mineralization rate for recalcitrant pools of N (c_r, µg g^{-1} d^{-1}). Lowercase letters (*a,b,c*) denote significant differences (P<0.05) between treatment means within a given parameter.

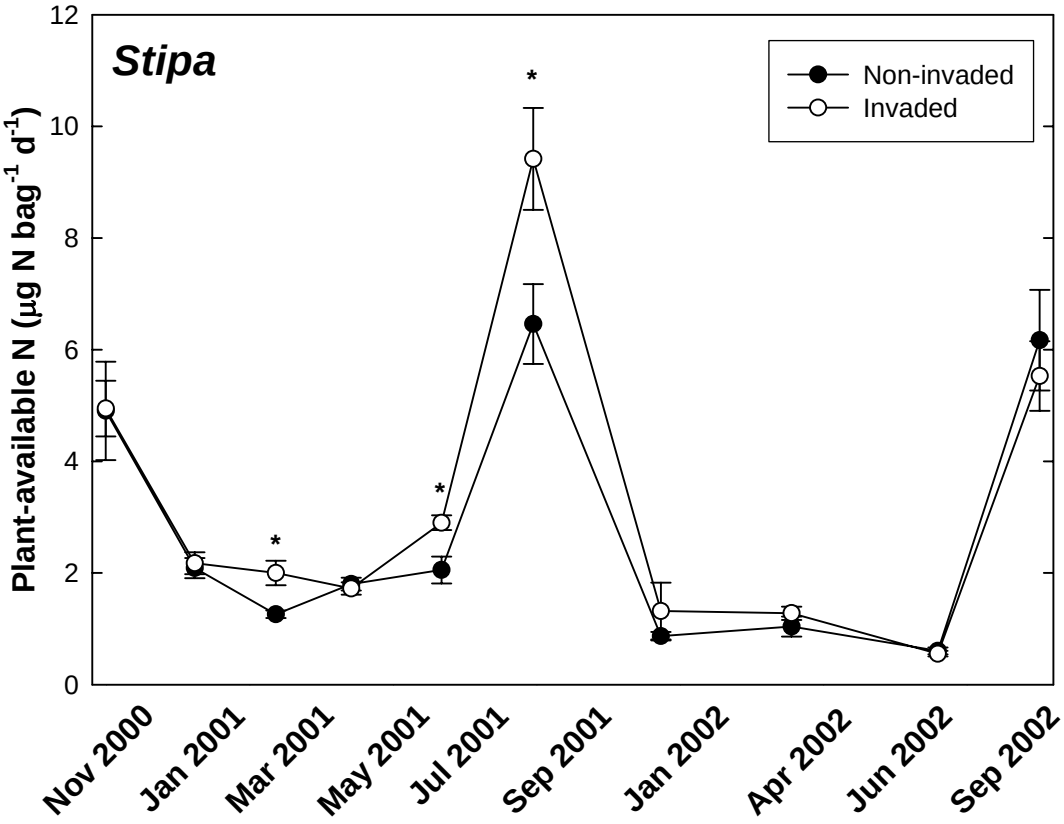


Figure 1. Mean plant-available N (NH_4^+ and NO_3^-) availability in intact and invaded stands of *Stipa* in Virginia Park. These data come from buried ion-exchange resin bags. Asterisks (*) denote sampling dates with significantly different resin N ($P < 0.05$). Bars represent standard error of the mean.

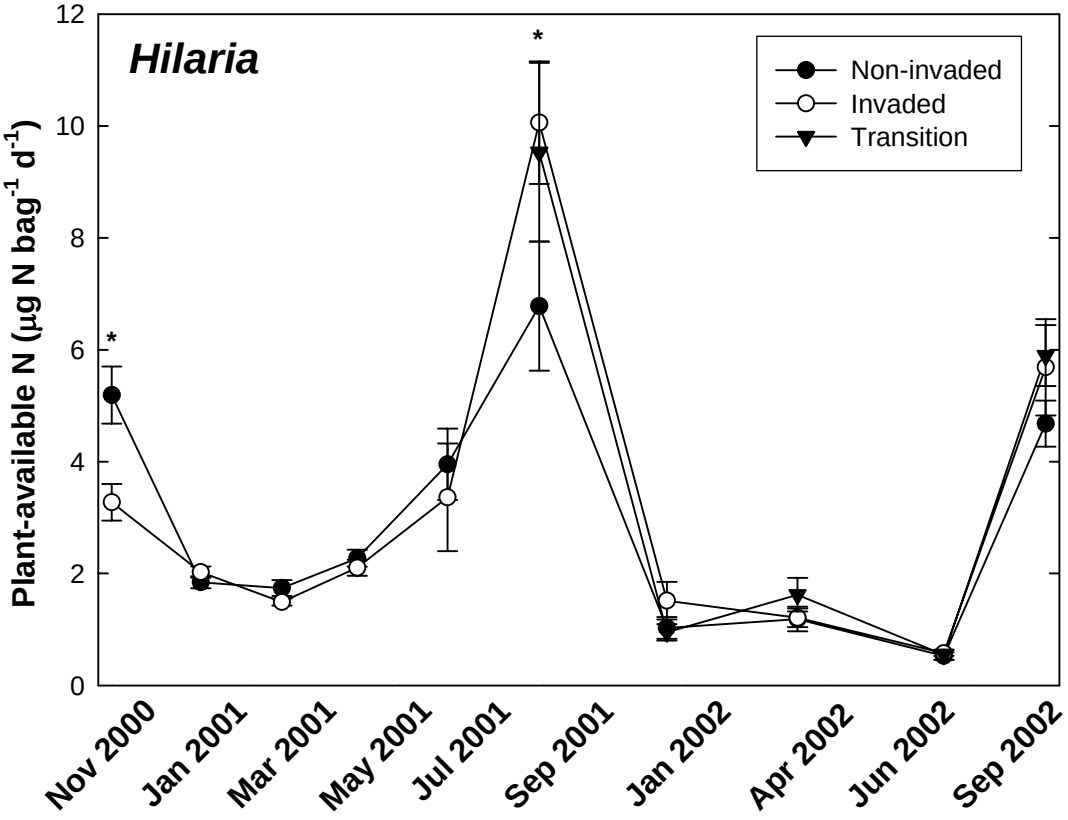


Figure 2. Mean plant available N (NH_4^+ and NO_3^-) availability in intact and invaded stands of *Hilaria* in Virginia Park. Transition sites are intact plots which were invaded over the course of the study. These data come from buried ion-exchange resin bags. Asterisks (*) denote sampling dates with significantly different resin N ($P < 0.05$). Bars represent standard error of the mean.

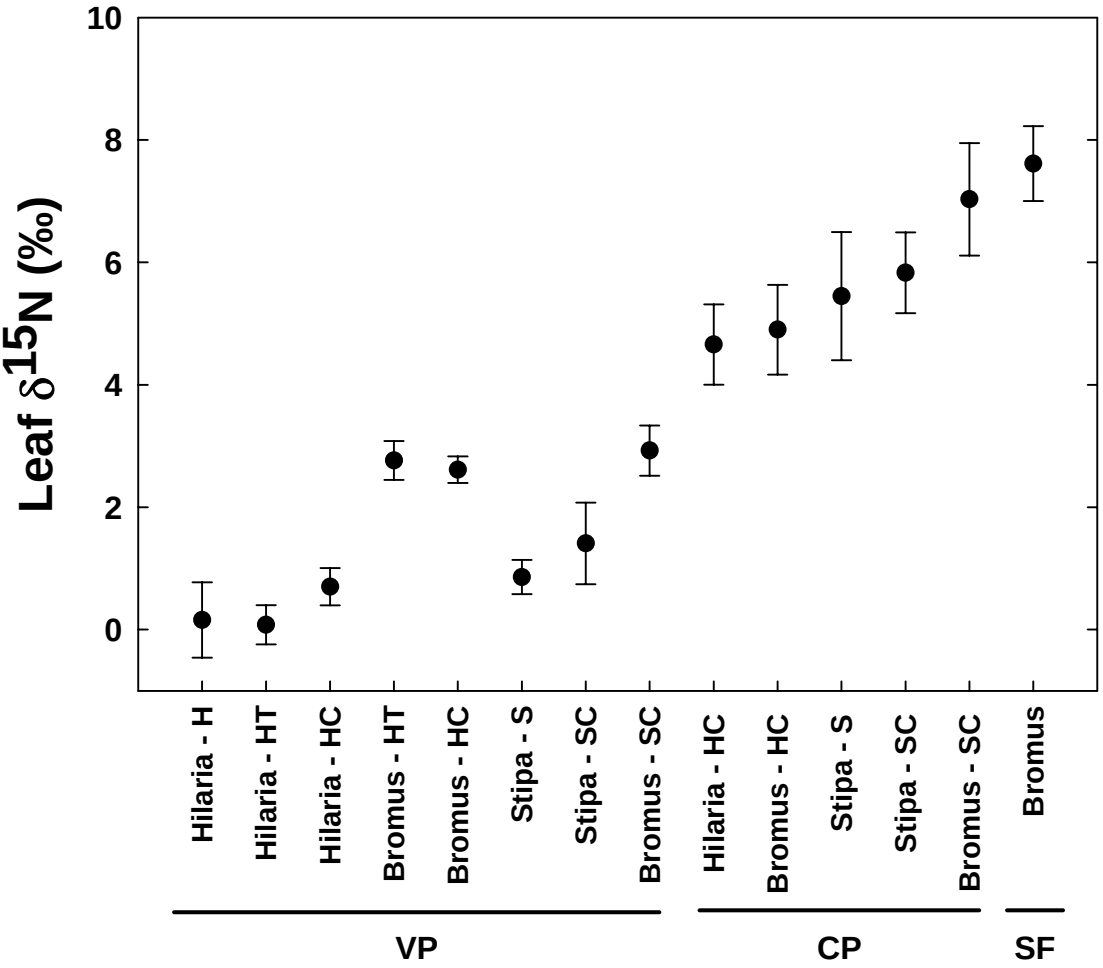


Figure 3. Mean leaf $\delta^{15}N$ for *Hilaria, Stipa,* and *Bromus* at three sites in Canyonlands National Park. The sites range from recently (<10 years) invaded (VP=Virginia Park), through CP=Chesler Park, to historically (>50 years) invaded (SF=Squaw Flat). Plots with each denote invasion status (H,S=non-invaded; HT=transition; HC,SC=invaded). Bars represent the standard error of the mean.

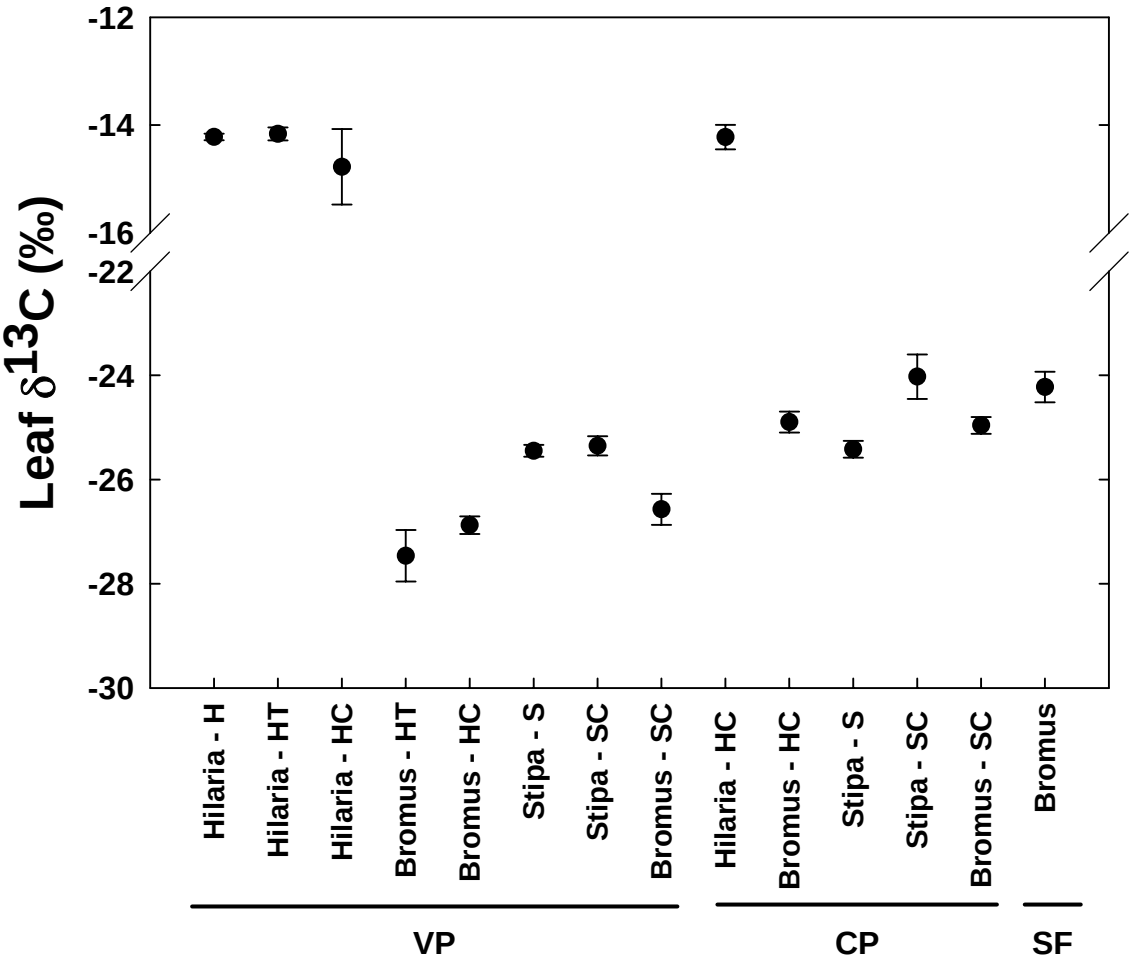


Figure 4. Mean leaf $\delta^{13}C$ for *Hilaria, Stipa,* and *Bromus* at three sites in Canyonlands National Park. The sites range from recently (<10 years) invaded (VP=Virginia Park), through CP=Chesler Park, to historically (>50 years) invaded (SF=Squaw Flat). Plots with each denote invasion status (H,S=non-invaded; HT=transition; HC,SC=invaded). Bars represent the standard error of the mean.

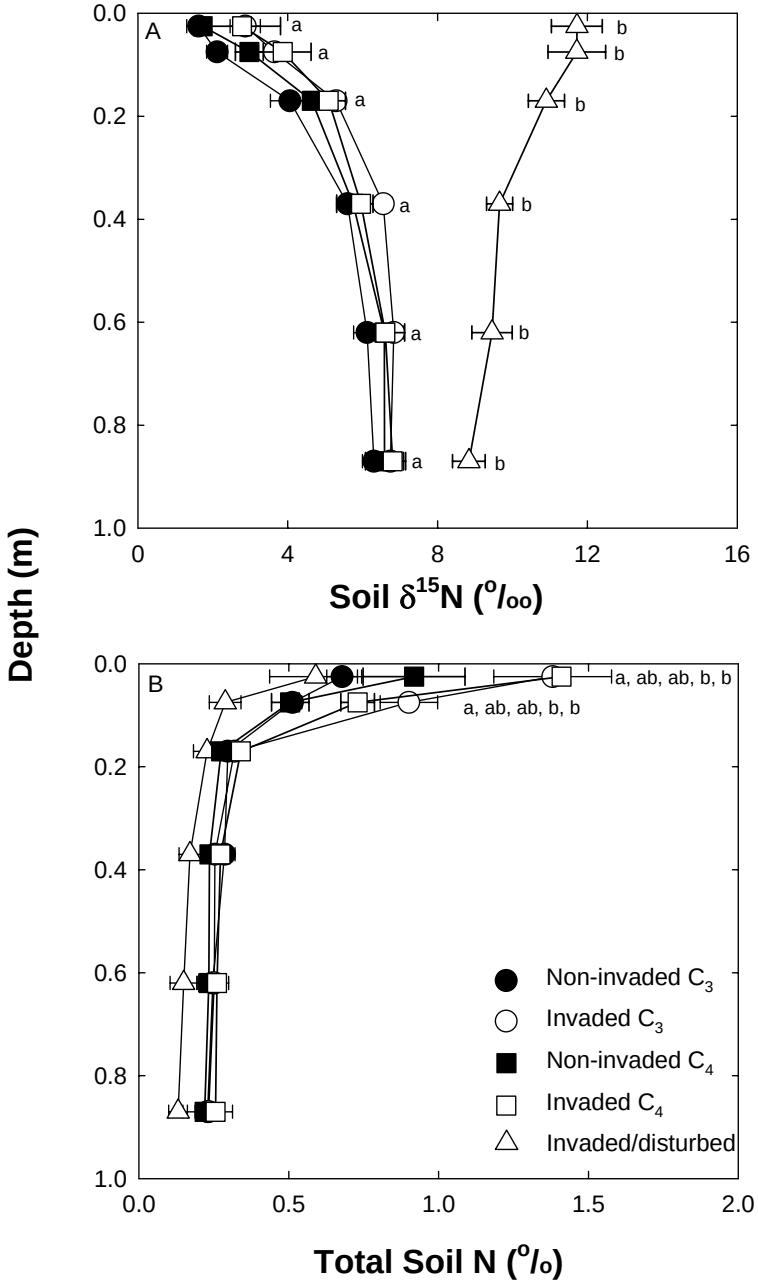


Figure 5. Mean (±SE) soil $\delta^{15}N$ (Panel A) and total N (Panel B) for 1 m soil cores from the non-invaded C_3 (*closed circles*), invaded C_3 (*open circles*), non-invaded C_4 (*closed squares*), invaded C_4 (*open squares*), and the invaded/disturbed communities (*open triangles*). Different letters indicate differences between communities at P<0.05; the non-invaded and invaded C_3 and C_4 communities were combined in panel A because there were no significant differences.

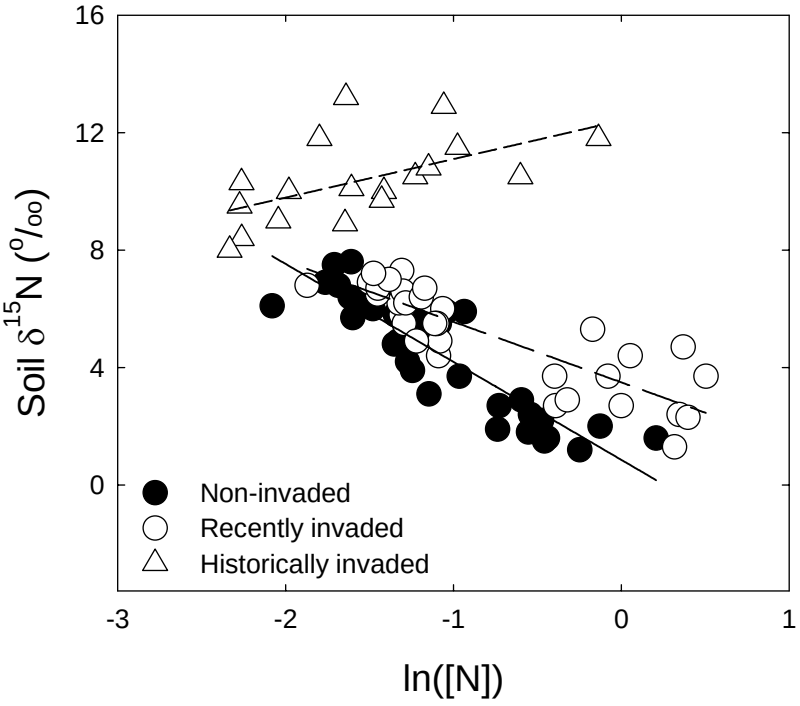


Figure 6. The Rayleigh Distillation Model is represented by the relationship between soil $\delta^{15}N$ and ln[N] from soils collected from 1 m soil cores from the non-invaded C_3 and C_4 (*closed circles*), recently invaded C_3 and C_4 (*open circles*), and the historically invaded/disturbed communities (*open triangles*). The slopes are significantly different for each community type (non-invaded: $\delta^{15}N = 0.83 - 0.90 * \ln [N]$, solid line; recently invaded: $\delta^{15}N = 3.50 - 0.86 * \ln [N]$, long dashed line; invaded/disturbed: $\delta^{15}N = 12.40 + 0.56 * \ln [N]$, short dashed line).

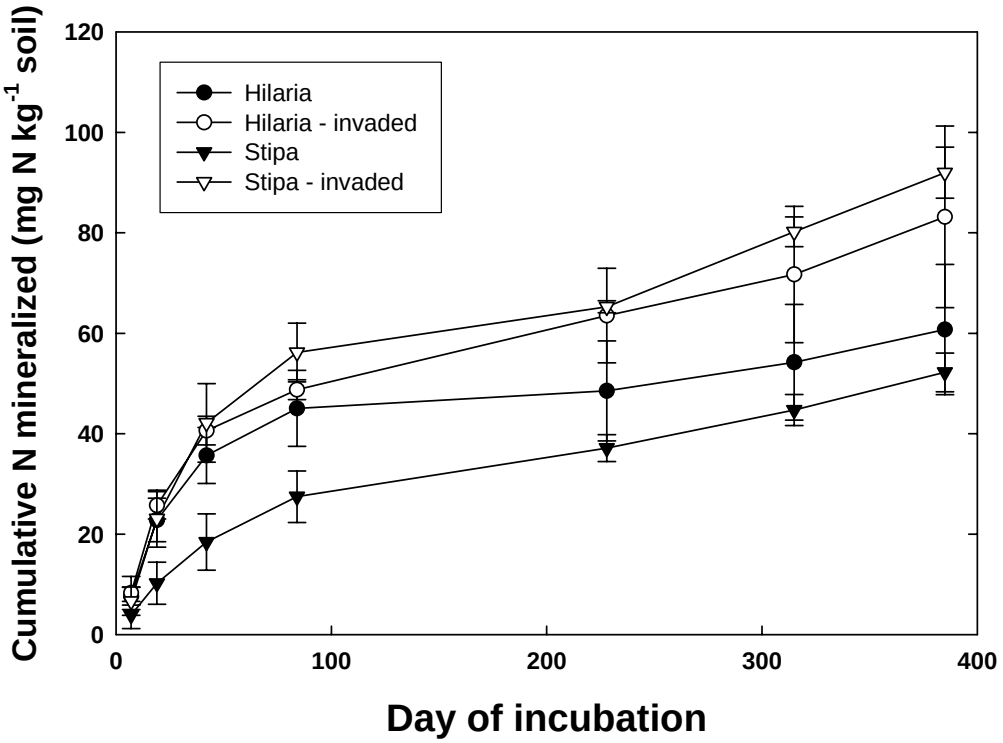


Figure 7. Mean net nitrogen mineralization (NH_4^+ and NO_3^-) a long-term soil incubation conducted in the laboratory. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. Bars represent the standard error of the mean.

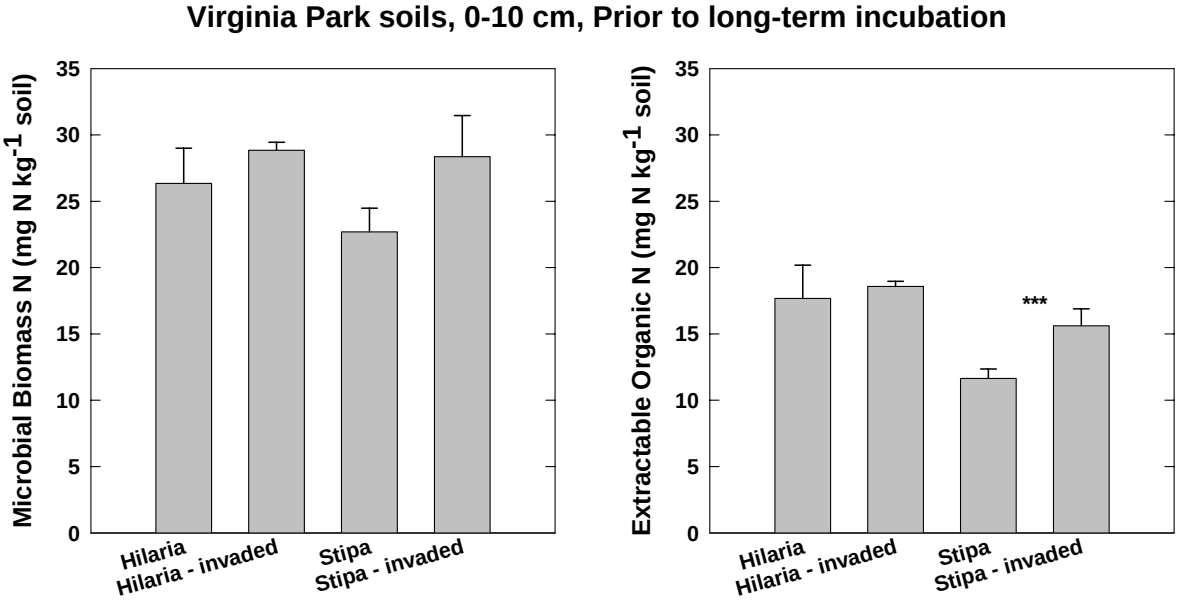


Figure 8. Mean microbial biomass N and organic N extractable in 0.5M K_2SO_4 from dry soils prior to long-term incubation. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. Asterisks (***) denote significantly different means ($P < 0.05$). Bars represent the standard error of the mean.

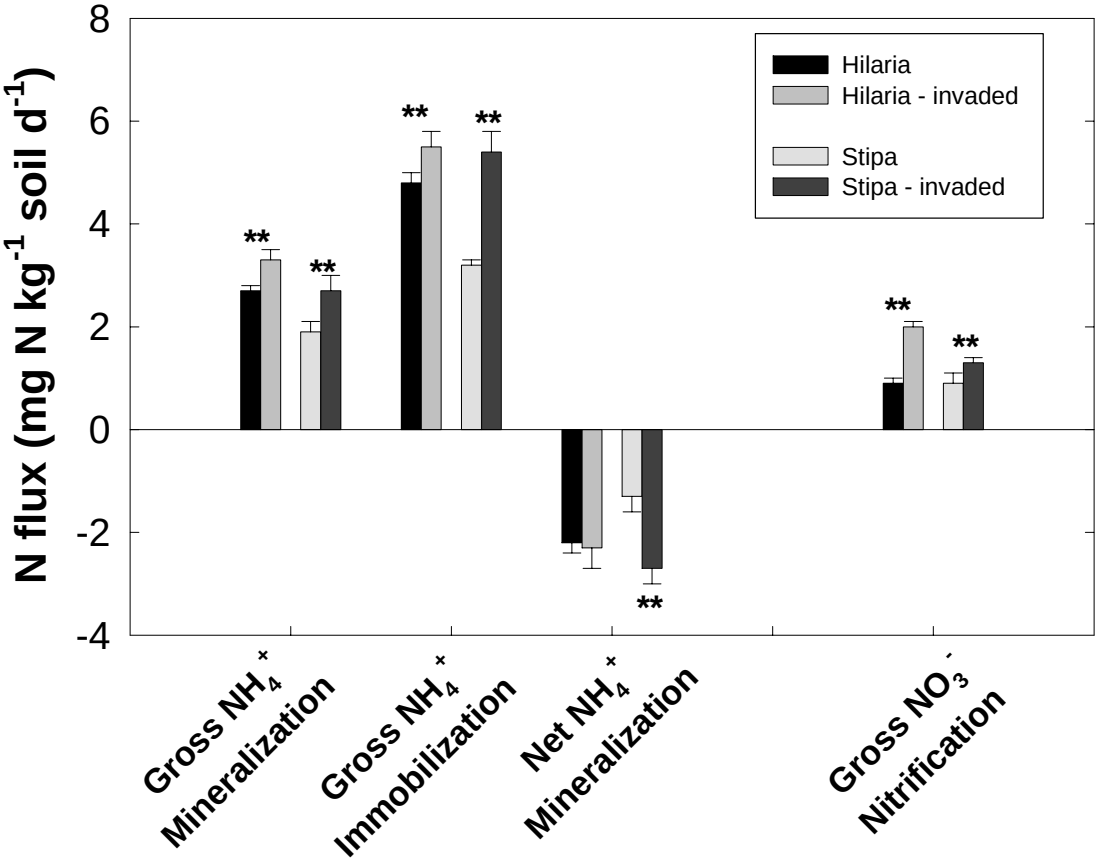


Figure 9. Mean gross and net N fluxes from dry soils prior to long-term incubation. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. Asterisks (**) denote significantly different means ($P < 0.05$). Bars represent the standard error of the mean.

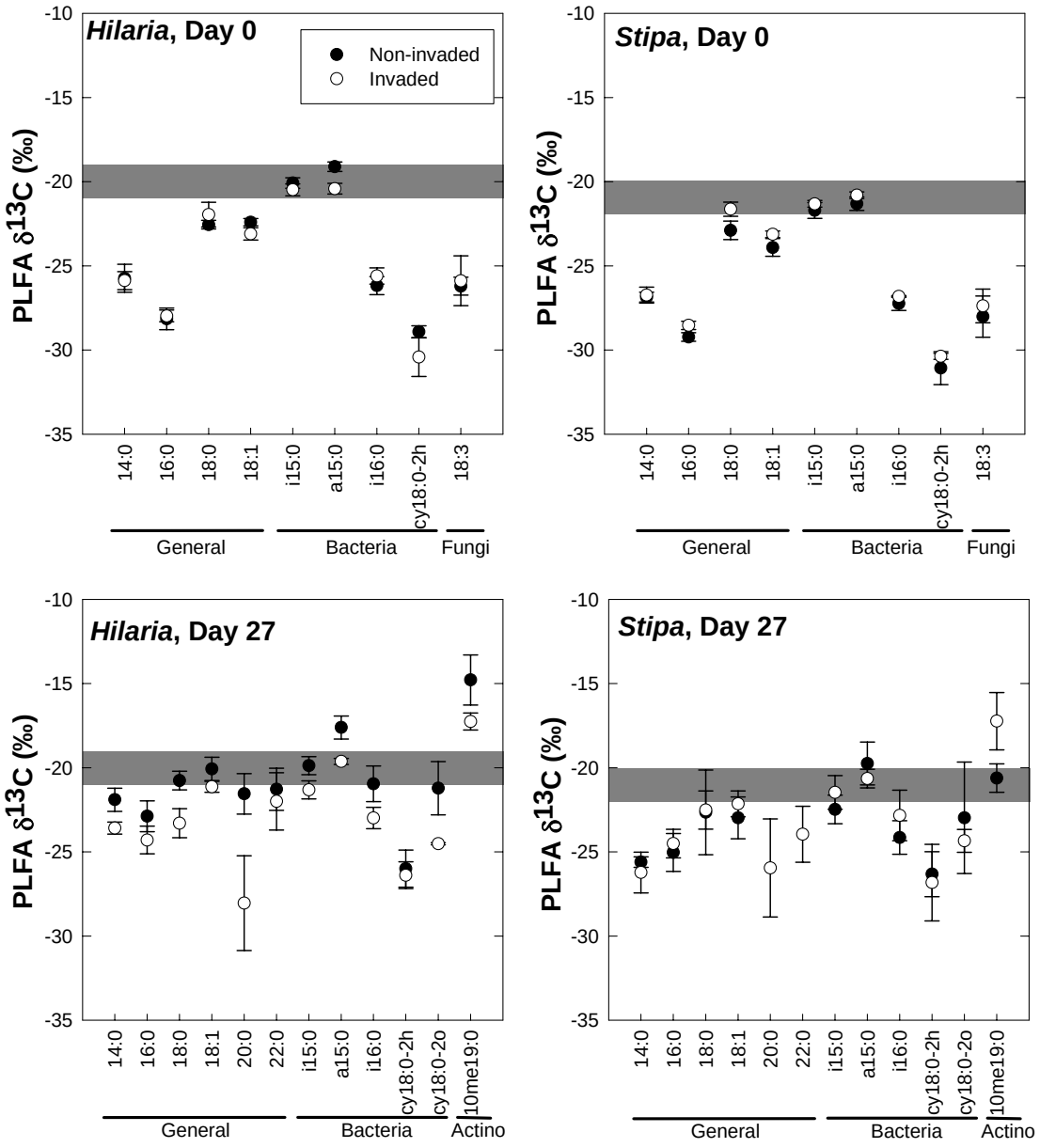


Figure 10. Mean $\delta^{13}C$ of soil microbial phospholipid fatty acids extracted from dry soils prior to long-term incubation and those 28 days into a long-term incubation. Fatty acid biomarkers are grouped according to the portion of the microbial community they represent (general, bacteria, fungi, and actinomycetes). Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. The shaded region is for reference and denotes the mean $\delta^{13}C$ of the bulk soil plus or minus one standard deviation. Bars represent the standard error of the mean.

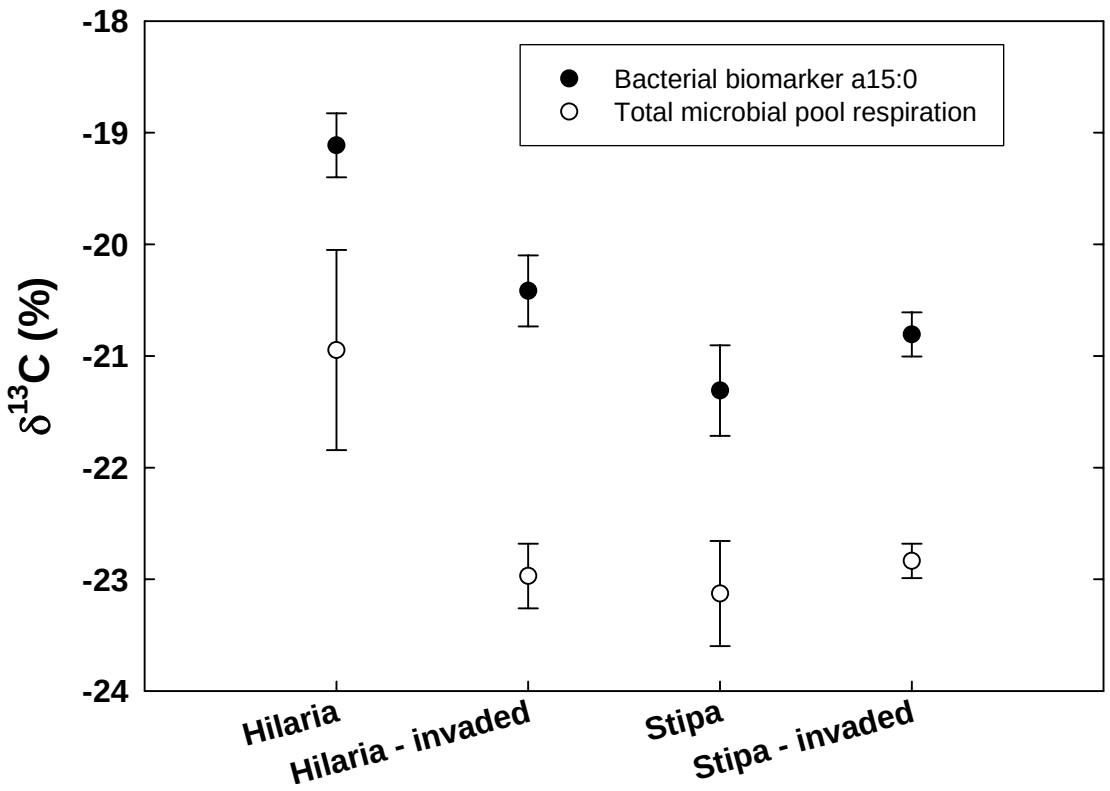


Figure 11. Mean $\delta^{13}C$ of respiration of total soil microbial pool relative to the mean $\delta^{13}C$ of the bacterial phospholipid fatty acid a15:0. Respiration values are for the first 24 h of the long-term incubation and fatty acid values are from dry soils prior to incubation. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. Bars represent the standard error of the mean.

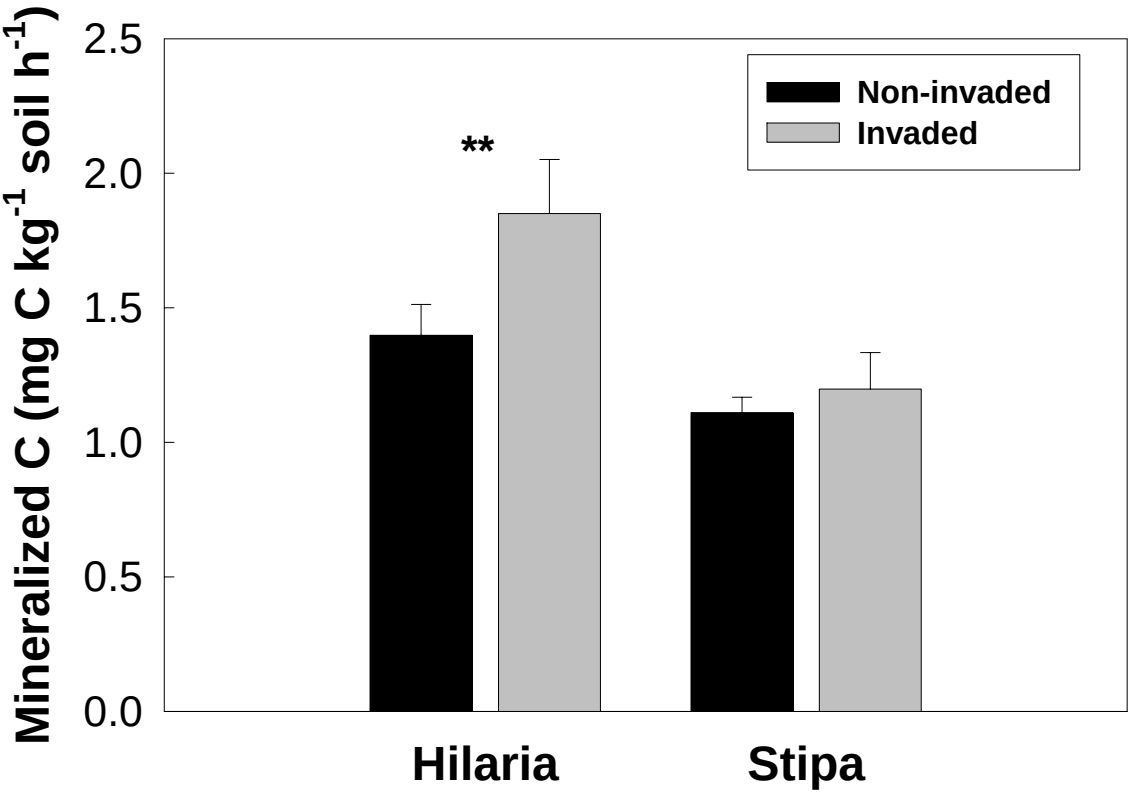


Figure 12. Mean C mineralization from microbial respiration. Respiration values are for the first 24 h of the long-term incubation. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. Asterisks (**) denote significantly different means between plots ($P < 0.05$). Bars represent the standard error of the mean.

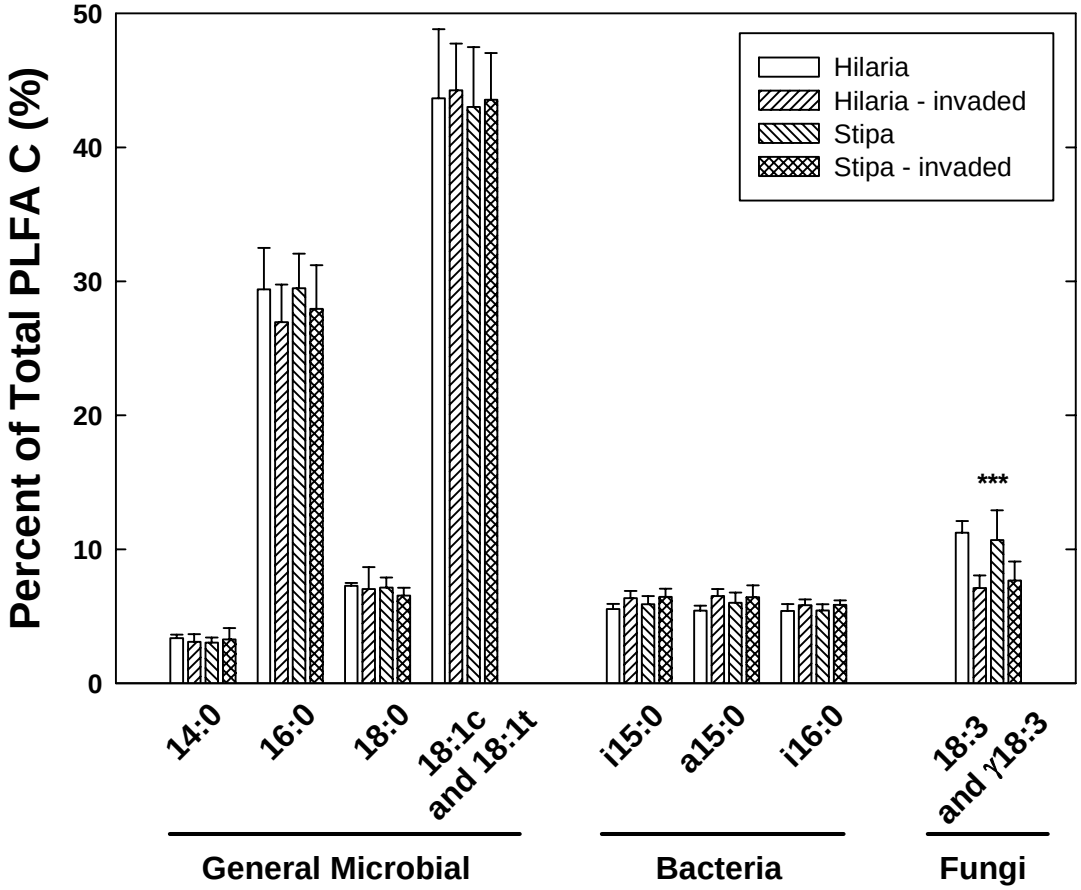


Figure 13. Mean relative abundance of the microbial community as expressed by the percent total phospholipid fatty acid (PLFA) C for selected biomarkers. Fatty acid values are from dry soils prior to incubation. Biomarkers fall into three groups: general microbial biomarkers, bacterial, and fungal. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. Asterisks (***) denote significantly different means between plots ($P < 0.05$). Bars represent the standard error of the mean.

Appendix A: Long-term incubation

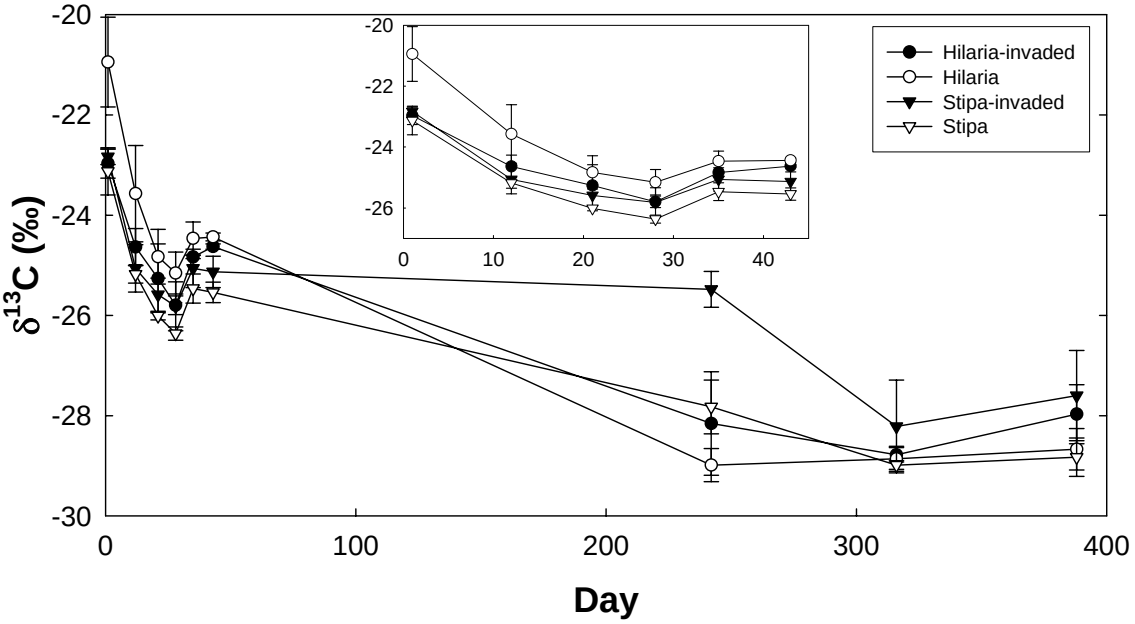


Figure 1. Mean $\delta^{13}C$ of soil respired CO_2 over the course a 388 d incubation of Virginia Park soils. Inset shows the first 42 d of incubation. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa* and incubated in the laboratory in sealed mason jars at 30ºC. Bars represent the standard error of the mean.

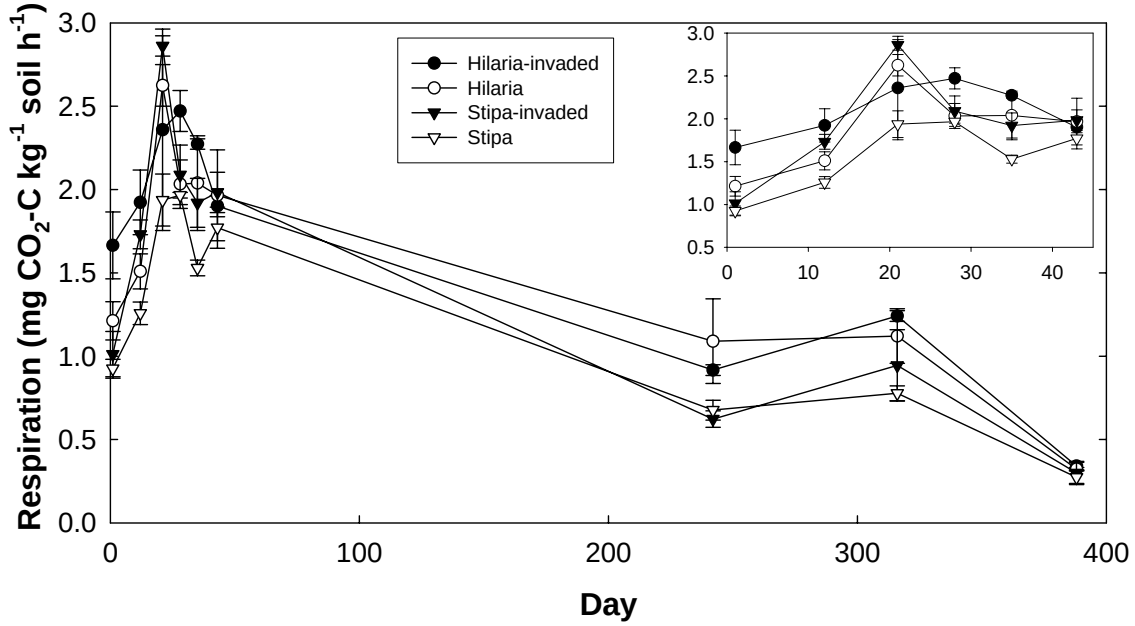


Figure 2. Mean soil respiration rates over the course a 388 d incubation of Virginia Park soils. Inset shows the first 42 d of incubation. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa* and incubated in the laboratory in sealed mason jars at 30ºC. Bars represent the standard error of the mean.

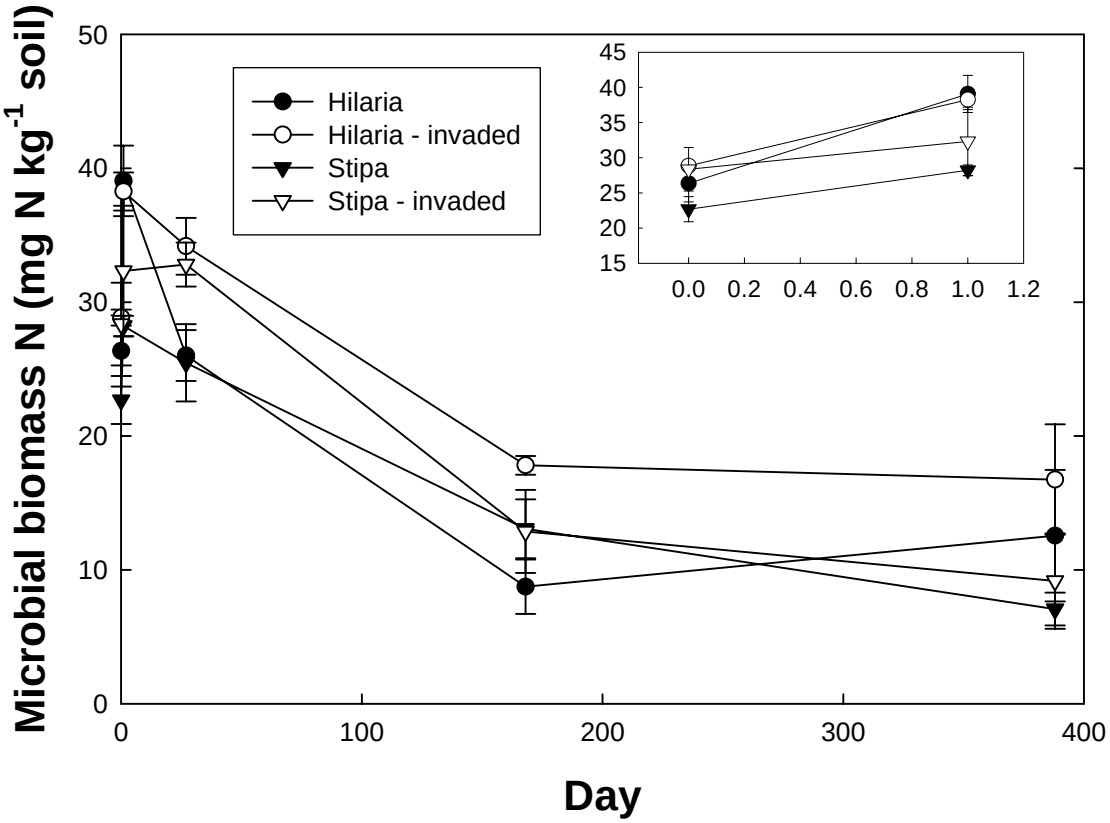


Figure 3. Mean microbial biomass N estimates using chloroform fumigation and extraction in 0.5M K_2SO_4 over the course a 388 d incubation of Virginia Park soils. Inset shows the biomass N from dry soils (day 0) and after 24 h incubation (day 1). Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa* and incubated in the laboratory in sealed mason jars at 30ºC. Bars represent the standard error of the mean.

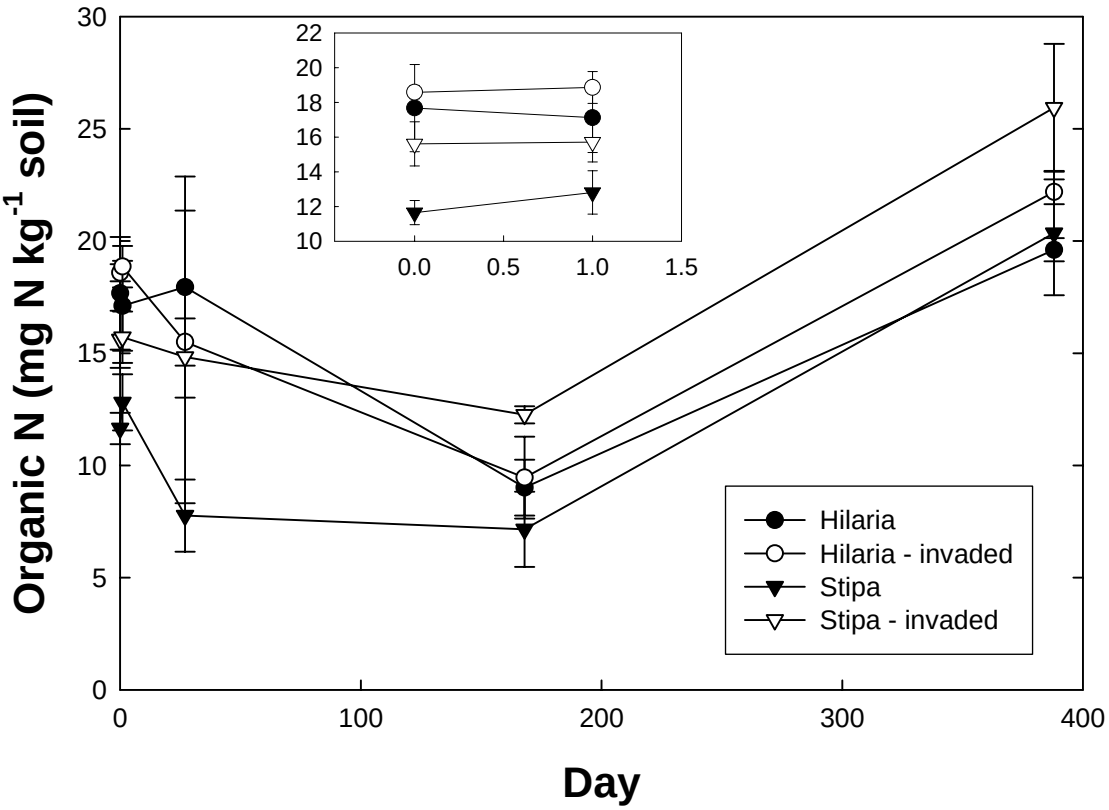


Figure 4. Mean organic N extractable in 0.5M K_2SO_4 estimates from non-fumigated soil extracts over the course a 388 d incubation of Virginia Park soils. Inset shows the biomass N from dry soils (day 0) and after 24 h incubation (day 1). Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa* and incubated in the laboratory in sealed mason jars at 30ºC. Bars represent the standard error of the mean.

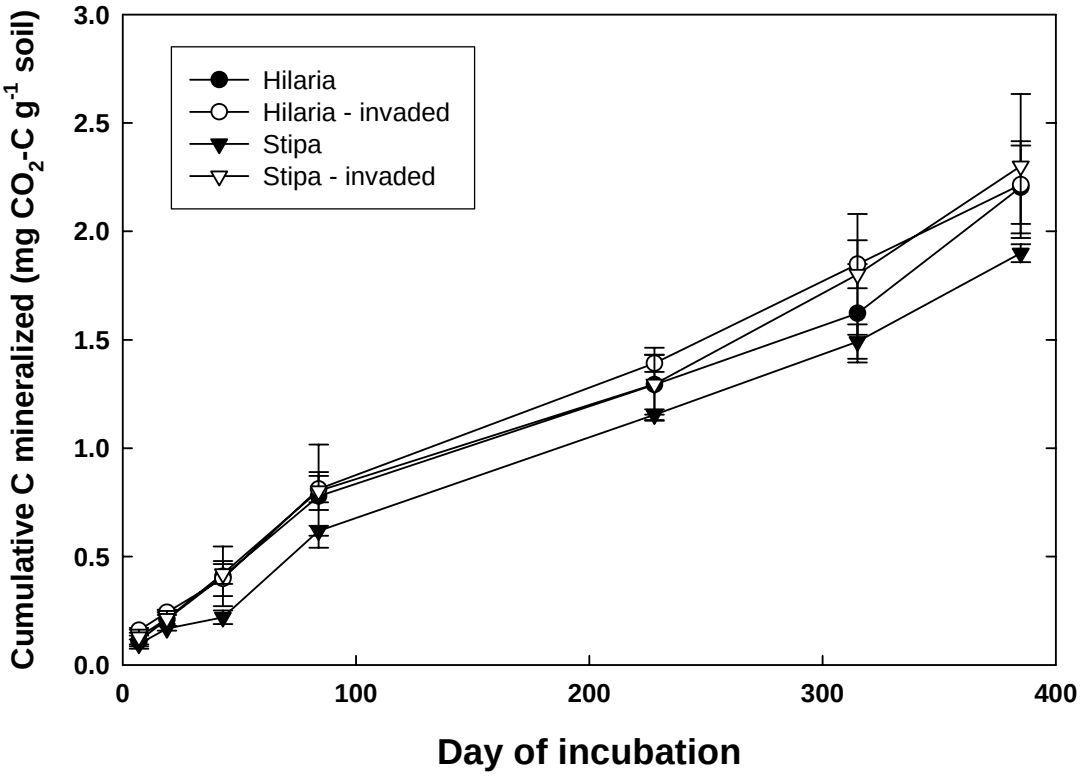
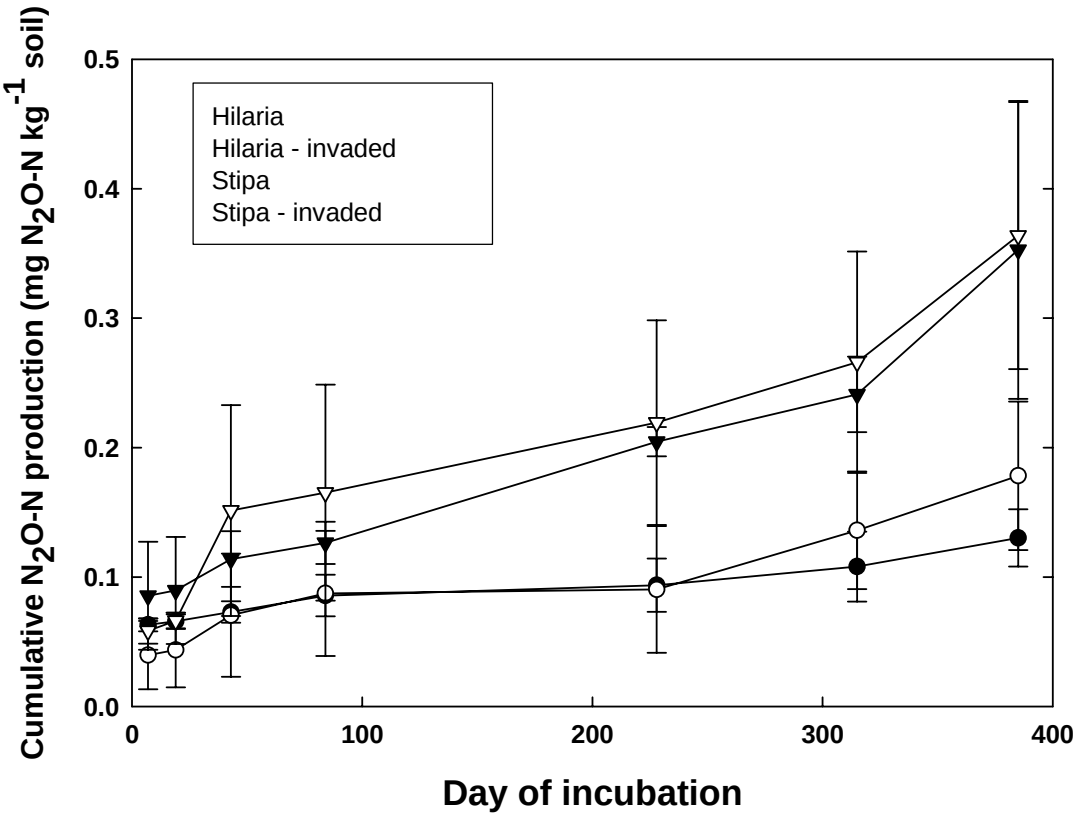


Figure 5. Mean net carbon mineralization from a long-term soil incubation conducted in the laboratory. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa* and incubated in the laboratory in sealed mason jars at 30ºC. Bars represent the standard error of the mean.



C

Figure 6. Mean net N_2O-N production from a long-term soil incubation conducted in the laboratory. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa* and incubated in the laboratory in sealed mason jars at 30ºC. Bars represent the standard error of the mean.

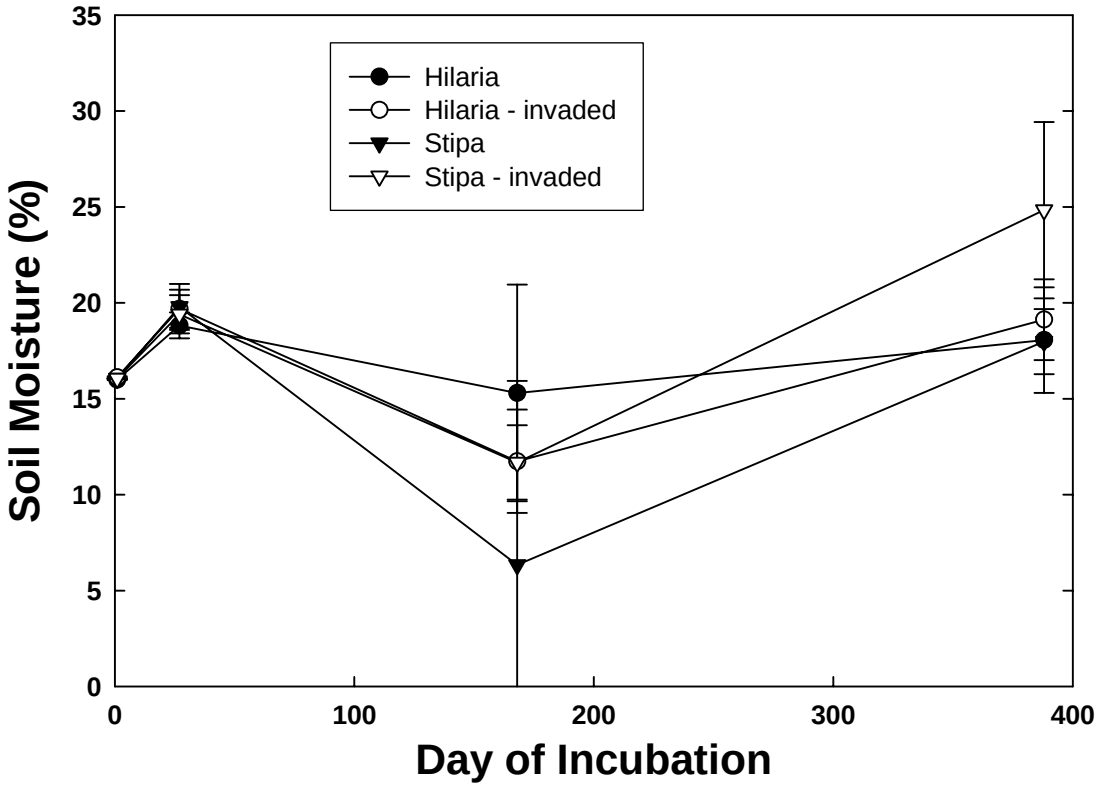


Figure 7. Mean soil moisture (%) from a long-term soil incubation conducted in the laboratory. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa* and incubated in the laboratory in sealed mason jars at 30ºC. Bars represent the standard error of the mean.

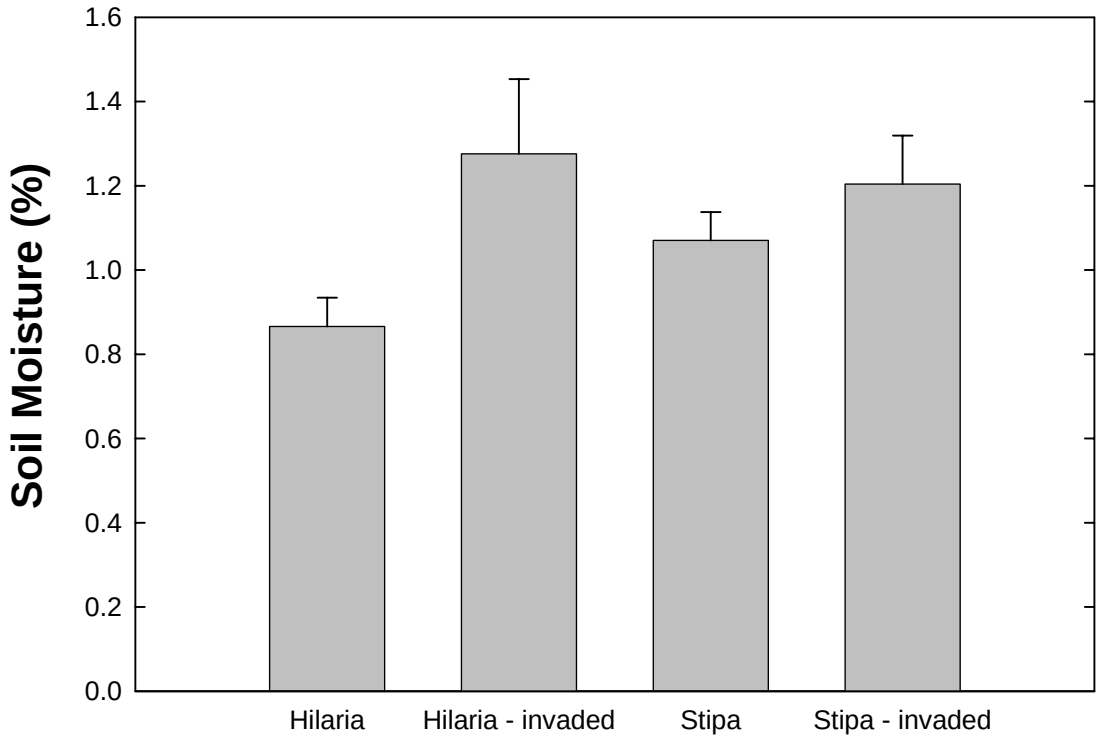


Figure 8. Mean soil moisture (%) from dry soils prior to a long-term soil incubation conducted in the laboratory. Soil cores (0 to 10 cm depth) were collected from non-invaded and invaded stands of *Hilaria* and *Stipa*. Bars represent the standard error of the mean.

The exotic annual grass *Bromus tectorum* alters soil food webs, soil processes, and plant community composition: does this ecological legacy preclude re-establishment of native plants?

Introduction

Ecological legacies have been recently defined as the physical structures (e.g., lava flows, landslides) and biological remnants (e.g., tree boles, seeds, fauna) left after large infrequent disturbances (LIDs) such as hurricanes, fires, and volcanic eruptions (Foster et al. 1998). Such remnants are proposed to leave an enduring legacy that influences subsequent community composition and ecosystem processes for decades to centuries following the disturbance. Finding emergent principles by which to predict the influence of ecological legacies requires characterizing and categorizing the composition and structure of the antecedent community, the timing and type of large disturbance, and the structure and function of the derivative landscape. The study of how exotic organisms affect native communities has been impeded by the lack of a conceptual framework by which to structure our inquiry into this issue. We propose that invasion of exotic plants and animals at the landscape scale fits the definition of a LID and that invasion is likely to leave behind ecological legacies that can influence the structure and function of subsequent communities. Therefore, the same conceptual structure used for investigations into ecological legacies could apply to invaded systems. Whereas including exotic invasions into the definition of legacy-creating agents does not call for creating new categories of antecedent communities, it does require expanding the current concept of disturbance type, and likely, the legacy type and resultant landscapes (for example, see characterization of LIDs in Foster et al. 1998). Having such a conceptual framework would be of great value to those attempting to predict invasion and restorationists, both of whom are faced with triage-type decisions such where to focus restoration efforts, what components are to be restored, and which type of restoration methods are to be used.

Many studies have examined the effect of invasive exotic plants on native plants and animals; however, only a handful of studies have focused on the effects of exotic plants on soil food webs (e.g., Kourtev et al. 2003, Ehrenfeld et al. 2001, Belnap and Phillips 2001). Because studies have found that different plants foster different soil food web organisms (Wardle 2002), it is to be expected that invasive plants, being new to the community, would also alter soil food composition and structure. We know of only one study that has addressed the specific effects of *Bromus* on soil food webs, and this study showed the presence of *Bromus* profoundly alters soil food webs within a few years after invasion (and in unexpected ways; Belnap and Phillips 2001). As soil food web composition and structure alters decomposition rates and thus soil nutrient availability, it is expected that changes in soil food webs will be reflected in vascular plant community structure and function. What type of changes in soil food webs are required to affect plant communities is currently of great debate: does a change in biodiversity or species richness alone affect ecosystem processes or plant community structure or are changes in particular species required for a change to manifest in plants? Is the functional redundancy found within soils sufficient to maintain normal functions, or is species composition of the soil food web important? Despite the importance of these questions, only a limited number of studies have directly asked whether (or which) alterations in soil food webs can affect vascular plant communities (Wardle 2002). Some noteworthy studies have been published in this arena, including ones showing that mycorrhizal fungi and microbial biomass can alter species composition and/or maintenance of biodiversity, nutrient capture, and productivity of plants (van

der Heijden et al. 1998. Grime et al. 1987). Modeling studies also suggest altered soil foodwebs can have a substantial impact on plant growth and species composition (Bever et al. 1997).

The presence of different plants can also directly alter soil nutrient availability. For example, root exudates can dissolve carbonates or lower soil pH, thus increasing phosphorus availability; roots can move nutrients and water from one soil zone to another; and differential element uptake by specific species can alters soil stoichiometric ratios which, in turn, can affect nutrient uptake rates in all plants (Sterner and Elsner 2002). Specific studies on how *Bromus* affects the availability of soil N and P have been equivocal. In the short-term, *Bromus* appears to increase available phosphorus in soils (Sanford in prep), total soil N and rates of decomposition, gross mineralization, gross nitrification, and denitrification (Ehrenfeld 2003, Booth et al. 2003, Evans et al. 2001, Bolton et al. 1990, Svejcar and Sheley 2001). However, these effects can vary seasonally and different studies show varying degrees of alteration. In addition, there is scant data on long-term effects.

Bromus tectorum L. (also called cheatgrass or downy brome; hereafter referred to as *Bromus*) is a C_3 annual grass that currently dominates 7 million acres of western US rangelands. It also occurs as a sub-dominant in most low elevation plant communities throughout the West. Where *Bromus* is the dominant plant, the type and timing of food and cover for animals is altered, native plant and animal diversity is reduced (Vail 1994), and wildfire cycles are greatly accelerated (Whisenant, 1990). The presence of *Bromus* has resulted in the endangerment of many plant and animal species (Rosentreter 1994). Consequently, finding ways to limit *Bromus* cover or to restore *Bromus*-dominated rangelands is of great importance to land managers. Exotic plant invasion will likely alter both soil food webs and chemistry and thus can be expected to affect native plant performance. The next step is to apply this to native systems: that is, how does the legacy of altered soil biota and chemistry affect the re-establishment of native species? Using a constructed, artificial system by adding known species is likely to give us an erroneous answer because knowledge of which species of soil-dwelling species are present under what conditions is too limited for accurate reconstruction. In addition, natural communities are a moving target, as their composition depends on factors at the time of community formation, including dispersal, competition, and abiotic conditions (Díaz et al. 2003), and these factors can change both spatially and temporally. Unfortunately, removal experiments can have similar problems to addition studies, especially in little-understood communities such as soil food webs. Knowing what species to remove requires knowledge of the conditions under which a species may be extirpated from the community. In addition, understanding how results from either type of manipulation can be applied to native systems is difficult, as it also requires in-depth knowledge of factors controlling the addition and/or removal of species. These problems support the use of field studies whenever possible.

In this study, we asked three questions using field studies: does *Bromus* alter soil food web structure and/or soil faunal biodiversity and does this affect re-establishment of native grasses? Secondly, does length of time of *Bromus* dominates a site influence this result? And thirdly, what is the relationship among richness of plant and soil species and ecological processes they influence? To answer these questions, we measured decomposition rates, species and abundance of bacteria, fungi, protozoa, nematodes, microarthropods, and soil abiotic characteristics in three naturally-occurring soils collected from adjacent sites with different invasion histories. We then grew the native perennial grass *Hilaria* in these three soils in the greenhouse and documented *Hilaria* germination, emergence and above- and below-ground biomass. By choosing to use a natural situation over an artificial one, we avoided the problems

discussed above, but also encountered microsite differences in soil texture and nutrients, as will be discussed below.

Methods

Canyonlands National Park (~1500 m above sea level) is located in a cold semiarid desert in southeastern Utah (avg. annual precipitation is 214 mm and annual average temperature is 12 ^{o}C; Miller 2000). This area has experienced substantial turnover of its landscape to communities dominated by *Bromus*. Previous work has shown that *Bromus* generally invades soils dominated by the perennial native C_4 rhizimatous grass *Hilaria jamesii* (hereafter referred to as *Hilaria*; Belnap and Phillips 2001, Belnap et al. 2003). These soils are slightly finer-textured and generally have higher levels of available potassium (K), phosphorus (P), and micronutrients than soils dominated by other native grasses found in this area (Kleiner and Harper 1977; Belnap et al. 2003). *Hilaria* is green during both spring and late summer-fall (Schwinning et al. 2002, West 1972), whereas *Bromus* is green only in spring. Both *Hilaria* and *Bromus* have a high concentration of roots in the top 20 cm of soil (Sperry et al., in prep). When *Hilaria* communities are invaded and simultaneously burned and/or grazed by livestock, *Hilaria* can be completely replaced with *Bromus*. In contrast, *Hilaria* plants in invaded areas that lack grazing or fire appear highly resistant to replacement by *Bromus* (Belnap et al. in prep).

In 1996 we laid out three replicate 30m x 30m plots within three vegetation types that had all once been dominated by *Hilaria*. The first vegetation type was one that is uninvaded and still dominated by *Hilaria*; the second type is one that was invaded in 1995 (hereafter referred to as the "recently invaded" site) and now consists of a mixture of *Hilaria* and *Bromus*; and the third is that was invaded at least 50+ years ago and now lacks *Hilaria* (hereafter referred to as the "50+ year" site; H. Redd, per. comm). The uninvaded and recently invaded sites were directly adjacent to each other. The 50+ year site was approximately 2 km away. Soils at all three sites are classified as Begay sandy loam soils. We have been measuring vegetation and soil chemistry bi-annually and soil food webs sporadically at these sites since 1996. At each sample time, vegetation cover by species and bioturbation was sampled in 25 0.25m^2 quadrats within each of the nine plots. At the same time, we collected composited soil samples (0-10 cm, 30 subsamples per composite). Soils were split into the appropriate number of parts, depending on the number of analyses being done. The first split was sent to Soil Food Webs, Inc. for analysis of active and total bacteria and fungi, protozoa, and/or nematodes. The second split was sent to Oregon State University (Andy Moldenke) for microarthropod analysis. The third split was sent to Brigham Young University Soil Laboratory for analysis of soil texture and chemistry, using standard laboratory techniques modified for high pH soils. Here we report values for protozoa and bacterial species in 1996; nematodes in 1996 and 2002; fungal species in 1997; active and total bacterial and fungal biomass in 2001 and 2002; and microarthropods in 2001. Decomposition cloths (standardized cotton strips; Latter and Harrison 1988) have been placed and removed monthly since 2002 at the uninvaded and recently invaded sites. Air temperatures and the timing and size of precipitation events were continuously recorded during the sampling times. Jack States (University of Wyoming) isolated and cultured fungal colonies on *Hilaria* and *Bromus* shoots.

For growing the native grass *Hilaria*, we collected composite soil samples from these same sites. Two splits were made from these samples. One split was was placed in pots to grow *Hilaria* in; the other was sieved at 2 mm and sent to the Brigham Young University Soil Laboratory for texture and chemical analyses. We repeated these growth trials twice. Each trial

consisted of 30 pots, with ten *Hilaria* seeds planted in ten replicates of the three soils. The first trial used seed from the National Resource Conservation Service (Los Lunas, NM). The seeds obtained were cleaned and thus only the caryopsis was present. Germination rates of these seeds was poor, averaging 33% in control soils. For the second trial, uncleaned seeds (with both the caryopsis and glumes) were obtained commercially from a nearby source (Southwest Seed, Inc., Dolores, CO). These germinated at an average rate of 72%. All pots and temperatures were monitored daily in the greenhouse and received deionized water when the soil surface dried. Average minimum and maximum temperatures during Trial 1 were 16 and 27 ¢C, respectively, while those for Trial 2 were 21 and 27 ¢C, respectively. Aboveground biomass of *Hilaria* was collected and weighed in both trials, whereas belowground biomass was collected from the first trial only.

Statistics were run using SPSS v.12 and PCOrd v.4.27. Data were first tested for normality using a Kolmogorov_Smirnov statistic, with a Lilliefors significance level for testing normality. Levene's test was used to examine the equality of variances, and both pooled and separate variance t-tests were used to examine for equality of means. Non-normal data was transformed, or if that was not possible, equivalent non-parametric tests were used. For the soil food web analysis, we used ANOVA, Sorensen's similarity index, and non-metric multidimensional scaling (NMS) ordination. For NMS, we used Sorenson distance measures to explore the relationship between different soil food web groupings. To determine appropriate ordination technique, beta diversity, skewness and coefficient of variation were determined for both columns (species) and rows (plot-year). NMS ordinations were run with a maximum of 400 iterations and a stability criterion of 0.0001 standard deviations in stress over the last 15 iterations. Each NMS was run at least five separate times to insure pattern stability. The Monte Carlo test was used to test stress and strength of the observed patterns. Pearson *r* and Kendall's tau bivariate correlation statistics were calculated to test relationship between NMS scores and environmental variables.

Speaman's rho rank correlation analyses and stepwise linear regressions models were used to corroborate the NMS results. Other analyses included a general linear model repeated measures that employed both univariate and multivariate analyses and a Type III sums of squares. None of our data met Mauchly's sphericity assumptions and so we used the Greenhouse_Geisser adjustment to validate the univariate F statistic. Between-plot effects were determined with Tukey's Honestly Significant Difference test. The repeated measures analysis was used to test for differences among years and plot type for each species. T- tests were used to compare plots with and without *Bromus* in the same year for the same species.

Numbers of germinating individuals were tested for differences among soils with single-factor ANOVA. Post-germination mortality was standardized to the number of germinating individuals, arcsin-transformed, and evaluated for differences among soils and between trials with analysis of covariance (ANCOVA) with the number of germinators as covariate. Root:shoot ratios and belowground and total biomass (Trial 1 only) and average aboveground individual biomass (Trial 1 and 2) were tested for differences among soils with number of survivors as the covariate. Differences discussed in the text are statistically significant ($P<0.05$) unless otherwise noted.

Results and Discussion

Greenhouse Hilaria *growth response*: There were no differences in *Hilaria* germination among soils ($F = 0.41$, $p = 0.66$; data not shown). Post-germination mortality showed no

significant differences between trials (F = 0.24, $p = 0.63$) or among soil source (F = 0.83, $p = 0.44$), and the number of germinators did not have a detectable effect on post-germination mortality (F = 0.14, $p = 0.71$; data not shown). Average aboveground *Hilaria* biomass was significantly different between trials (F = 18.82) and among soils (F = 12.32), with above-ground biomass consistently greatest in the 5-year invaded soils (Figure 1). In Trial 1, we also measured below-ground biomass. We found no differences among soils (F = 1.22, $p = 0.31$; Figure 2) or root-shoot ratios (F = 0.09, $p = 0.92$; data not shown).

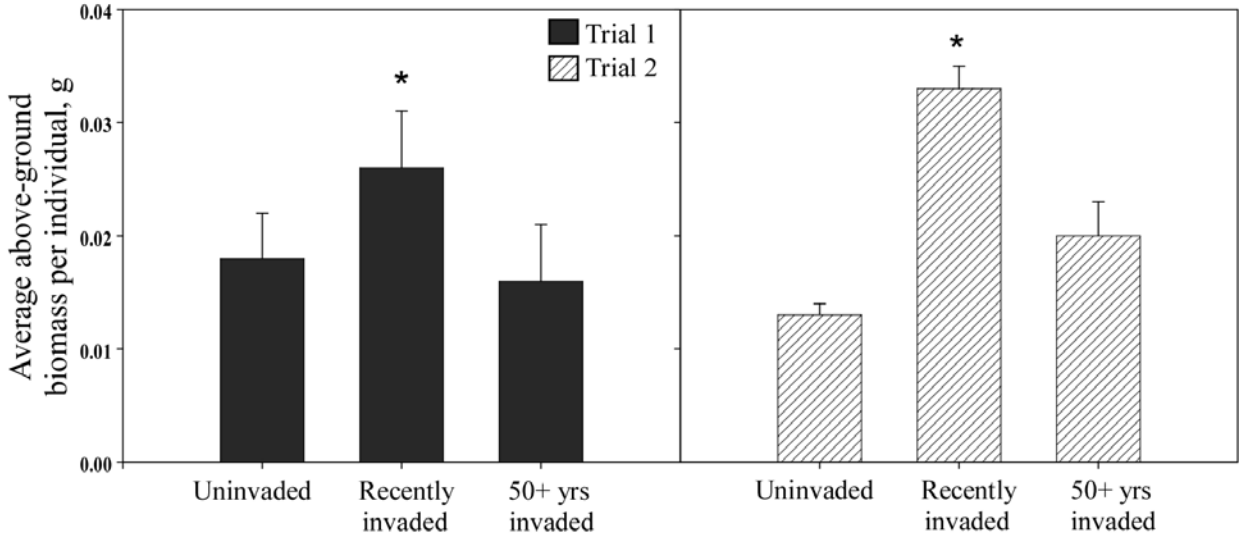


Figure 1. Above-ground *Hilaria* biomass (two trials) grown in soils from the uninvaded, recently invaded, and 50+ year invaded sites. Note that *Hilaria* biomass is consistently higher when grown in soils from the recently invaded site.

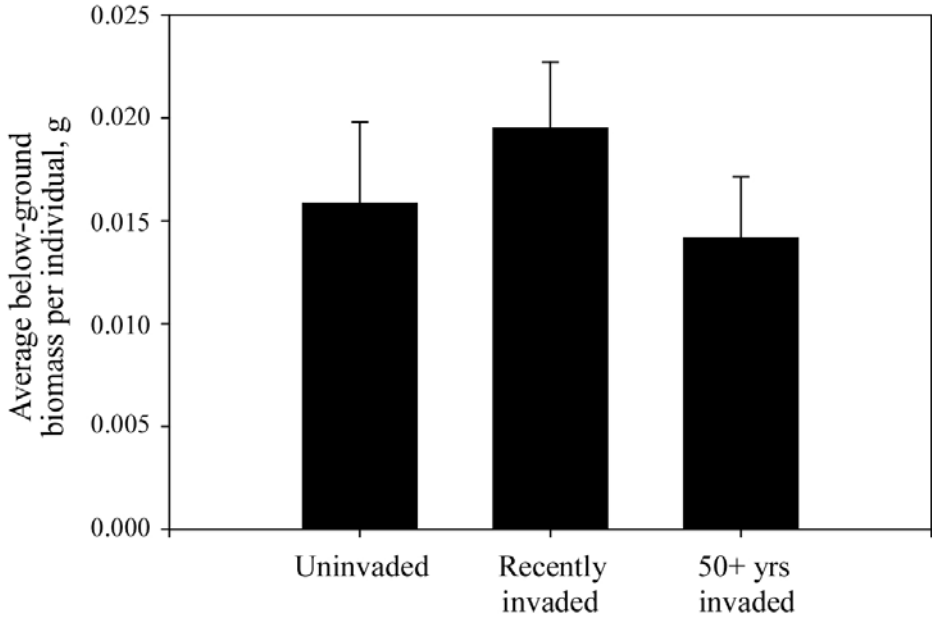


Figure 2. Below-ground *Hilaria* biomass grown in soils from the uninvaded, recently invaded, and 50+ year invaded sites.

Soil food webs: Differences in soil biota among sites did not mirror observed differences in *Hilaria* biomass among sites, thus indicating there was no clear connection between soil food web organisms' abundance or composition and *Hilaria* performance. To demonstrate such a correlation, we would have expected patterns in the soil food web organisms among sites to be similar to patterns of *Hilaria* biomass: that is, organisms in the recently invaded soil would be expected to be significantly different than the other two soils. However, this did not occur among any soil biotic group in any year, with one exception (total nematodes in 1996). In 2001, active bacteria and active/total bacteria ratios were higher in the 50+ year site compared to the other two sites (Table 1). In 2002, active fungi and active/total fungai ratios were higher at the 50+ year invaded site relative to the other two soils. There were no significant differences in the other microbial measures. Richness of fungal species found on *Hilaria* shoots were higher in the uninvaded site (13 in spring, 15 in fall) than the recently invaded site (10 in spring, 11 in fall), whereas richness of species on *Bromus* shoots was similar between the recently invaded (9 species) and 50+ year site (8 species; Table 2). It is interesting to note that saprobic fungi occur more commonly on *Bromus*, whereas facultative pathogens are more common on *Hilaria* (J. States, unpublished report). No significant differences were seen in ciliates, flagellates, amoebae, or total protozoa abundance among the sites (Table 3).Thus, neither microbial or protozoan numbers followed the pattern observed in *Hilaria* biomass.

		2001			2002		
	Invasion status	**Mean**	**Std. error**	***P***	**Mean**	**Std. error**	***P***
Active Bacteria	Uninvaded	6.82 [ab]	0.74	**0.10**	5.13 [a]	0.61	**0.01**
	Recently invaded	6.38 [a]	0.35		3.17 [a]	1.33	
	50+ years invaded	8.33 [b]	0.85		12.47 [b]	1.56	
Total Bacteria	Uninvaded	145	5	0.64	92	8	0.39
	Recently invaded	152	6		113	8	
	50+ years invaded	147	3		130	24	
Active Fungi	Uninvaded	3.20 [a]	0.93	**0.05**	0.21	0.21	0.39
	Recently invaded	3.47 [a]	0.26		0.19	0.09	
	50+ years invaded	5.86 [b]	1.25		1.41	0.99	
Total Fungi	Uninvaded	188	37	0	20	2	0.14
	Recently invaded	109	11		30	4	
	50+ years invaded	178	50		21	3	
Total Fungi:Total Bacteria	Uninvaded	1.29 [b]	0.24	**0.10**	0.22	0.04	0.39
	Recently invaded	0.73 [a]	0.09		0.27	0.03	
	50+ years invaded	1.24 [b]	0.38		0.18	0.05	
Active Fungi:Total Fungi	Uninvaded	0.021 [a]	0.007	**0.02**	0.012	0.012	0.42
	Recently invaded	0.032 [ab]	0.002		0.006	0.003	
	50+ years invaded	0.047 [b]	0.014		0.077	0.059	
Active Bacteria:Total Bacteria	Uninvaded	0.047 [ab]	0.005	**0.08**	0.057 [ab]	0.012	**0.04**
	Recently invaded	0.042 [a]	0.003		0.027 [a]	0.011	
	50+ years invaded	0.057 [b]	0.006		0.101 [b]	0.018	
Active Fungi:Active Bacteria	Uninvaded	0.50	0.16	0.17	0.05	0.05	0.74
	Recently invaded	0.55	0.05		0.05	0.03	
	50+ years invaded	0.74	0.16		0.10	0.06	

Table 1. Active and total bacteria and fungi (?g/g soil) from the uninvaded, recently invaded, and 50+ year invaded sites in 2001 and 2002.

Species	*Hilaria*				*Bromus*	
	Spring		Fall		Spring	
	Uninvaded	50+ yrs invaded	Uninvaded	50+ yrs invaded	Recently invaded	50+ yrs invaded
Acremonium spp.	11	44	33	33	67	42
Alternaria spp.	100	100	100	92	83	100
Arthrobotrys sp.				17		
Aureobasidium			33		8	33
Bipolaris spicifera	22	11	83	50		
Bipolaris sp.	33		25	8		
Bispora sp.					8	33
Chaetomium aureum	22		8		33	
Cladosporium spp.	44		42		67	100
Epicoccum nigrum	56			17	33	
Embellisia spp.	56	11	8			
Fusarium sp. #2	11	33				
Fusidium sp.?	11	11	50			
Penicillium spp.						100
Phoma sp.	11	56	42	33	13	83
Platyspora permunda?			8	33		
Rhizopus oryzae		22	44	50	83	22
Sphaeropsidales spp.	22		25	17		
Stagonospora sp.			44	17		
Ulocladium spp.			33			
Sterile white-gray	44	11				
Sterile white cottony		44				

[a] Frequency calculated on basis of 9 fall samples and 12 spring samples for each site

Table 2. Dominant fungi (>10% frequency) on live *Hilaria* and *Bromus* roots at the uninvaded, recently invaded, and 50+ year invaded sites. Notice that *Hilaria* shoots in the uninvaded sites had a greater number of fungal species than the 50+ year invaded sites both in spring and fall.

Type	Uninvaded	Recently invaded	50+ yrs invaded
Flagellates	12 ± 3	316 ± 249	15 ± 4
Amoebae	294 ± 149	180 ± 54	486 ± 377
Ciliates	3 ± 1	21 ± 14	10 ± 6
Total protozoa	308 ± 149	518 ± 240	510 ± 376

Table 3. Numbers of flagellates, amoebae, and ciliates per gram of fresh soil at the uninvaded, recently invaded, and 50+ year invaded sites. There were no significant differences among the sites within a group.

Type	Species	Spring 1996 Uninvaded	Spring 1996 Recently invaded	Spring 1996 50+ yrs invaded	Spring 2002 Uninvaded	Spring 2002 Recently invaded	Spring 2002 50+ yrs invaded
BACTERIAL-FEEDERS	*Acrobeles*				1.02 ± 0.44	0.26 ± 0.06	0.26 ± 0.08
	Acrobeloides				0.21 ± 0.13	0.02 ± 0.01	0.29 ± 0.10
	Acrobelophis				0.11 ± 0.06	0.02 ± 0.01	0.04 ± 0.03
	Cephalobus				0.02 ± 0.02	0.00 ± 0.00	0.03 ± 0.03
	Chiloplacus				0.23 ± 0.06	0.03 ± 0.01	0.04 ± 0.02
	Cervidellus				0.09 ± 0.04	0.03 ± 0.02	0.04 ± 0.01
	Total	1.12 ± 0.15 [b]	0.74 ± 0.10 [a]	1.16 ± 0.17 [b]	1.67 ± 0.75 [a]	0.37 ± 0.11 [b]	0.72 ± 0.27 [b]
FUNGAL-FEEDERS	*Eudorylaimus*				0.04 ± 0.01	0.03 ± 0.01	0.03 ± 0.01
	Thonus				0.03 ± 0.01	0.00	0.00
	Thornia				0.00	0.01 ± 0.01	0.00
	Total	0.27 ± 0.05	0.25 ± 0.04	0.16 ± 0.04	0.07 ± 0.02	0.04 ± 0.02	0.03 ± 0.01
FUNGAL/ROOT-FEEDERS	*Aphelenchus*				0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02
	Aphelenchoides				0.13 ± 0.06	0.02 ± 0.01	0.00
	Ditylenchus				0.19 ± 0.08	0.01 ± 0.00	0.00
	Tylenchus				0.36 ± 0.06	0.06 ± 0.03	0.00
	Total	0.45 ± 0.06	0.46 ± 0.08	0.28 ± 0.07	0.69 ± 0.20 [a]	0.10 ± 0.05 [b]	0.02 ± 0.02 [b]
ROOT-FEEDERS	*Helicotylenchus*				0.05 ± 0.05	0.00	0.00
	Meloidogyne				0.00	0.01 ± 0.00	0.00
	Tylenchorhynchus				0.03 ± 0.03	0.00	0.00
	Total				0.09 ± 0.09	0.01 ± 0.00	0.00
TOTAL		1.84 ± 0.22	1.45 ± 0.19	1.60 ± 0.26	2.51 ± 1.05 [a]	0.52 ± 0.18 [b]	0.76 ± 0.30 [b]

Table 4. Nematodes (number/gram of fresh soil) in soils from the uninvaded, recently invaded, and 50+ year invaded sites in both 1996 and 2002.

There was no observed difference among sites for total nematode abundance in 1996 (Table 4). Bacterial-feeding nematode abundance was higher in the uninvaded and 50+ year site compared to the recently invaded site, the only instance in which soil biotic patterns reflected that of *Hilaria* biomass patterns. However, this difference was not consistent through time. In 2002, bacterial-feeding nematode abundance was still highest in the uninvaded site, but not different between the recently invaded and 50+ year sites. In 2002, numbers of fungal or root feeding nematodes was not different among sites in either year. Numbers of root/fungal feeders were not different in 1996. However, in 2002, there were more root/fungal feeders and total nematodes in the uninvaded than either the 5 or 50+ year sites. Nematode species richness was similar in the non-invaded (14 species) and the recently invaded (13 species) site, but was lower in the 50+ year site (8 species). Therefore, only one of many nematode comparisons were similar to the pattern of *Hilaria* biomass.

The composition and abundance of microarthropods showed large differences among the sites; however, the pattern of these differences also did not conform to the pattern of *Hilaria* biomass (Figure 3). The uninvaded soil contained 16 species of microarthropods, whereas the recently invaded site had 12 species and the 50+ year site had only four species present. Species composition was quite different among the soils, as only two species occurred in all three sites (the herbaceous arthropod *Tortricid* and the mite *Oppiella*) and only six species occurred in two sites. Whereas the 50+ year site was more a depauperate version of the recently invaded site, there was a large difference in species between the uninvaded and recently invaded site, as only six species were common between the sites. At the recently invaded site, six new species had appeared and seven were lost with *Bromus* dominance. In the instances where species were common across soils, the uninvaded site had the greatest abundance of a given species. As with microbe, protozoa, and nematodes, neither the composition or abundance of microarthropods fit the pattern of *Hilaria* biomass.

When all soil food web data was analyzed with NMS, the two invaded sites clumped together and the uninvaded site was quite separate (Figure 4). This is clearly not the same pattern as that of *Hilaria* biomass, where soils from the not invaded and 50+ year site produced similar

biomass. Instead, the similarities in soil food webs were between the 5 and 50+ year sites, with the not invaded site being quite separate. (For discussion of soil chemistry differences among sites, see below).

Field measures of plant species richness and decomposition rates: Plant species richness varied with precipitation in the uninvaded and recently invaded plots; however it was always lowest in the 50+ year site (Table 5). In years with average precipitation, richness was highest in the uninvaded plots, intermediate in the recently invaded plots, and lowest in the 50+ year plots. In dry years, richness was equal among the uninvaded and recently invaded plots. As with soil food webs, this pattern did not mirror the pattern seen in *Hilaria* biomass grown in these soils. Decomposition rates were not significantly different between the uninvaded and recently invaded sites (Figure 5). Maximum decomposition appeared correlated with the time of year when plants are inactive and when air temperatures are highest, rather than timing or amount of precipitation. Because we did not measure decomposition rates in the 50+ year sites, we do not know if decomposition rates follow the observed pattern of *Hilaria* biomass. However, it is clear that decomposition rates did not correlate with species richness or abundance of microarthropods, nematodes, or root fungi.

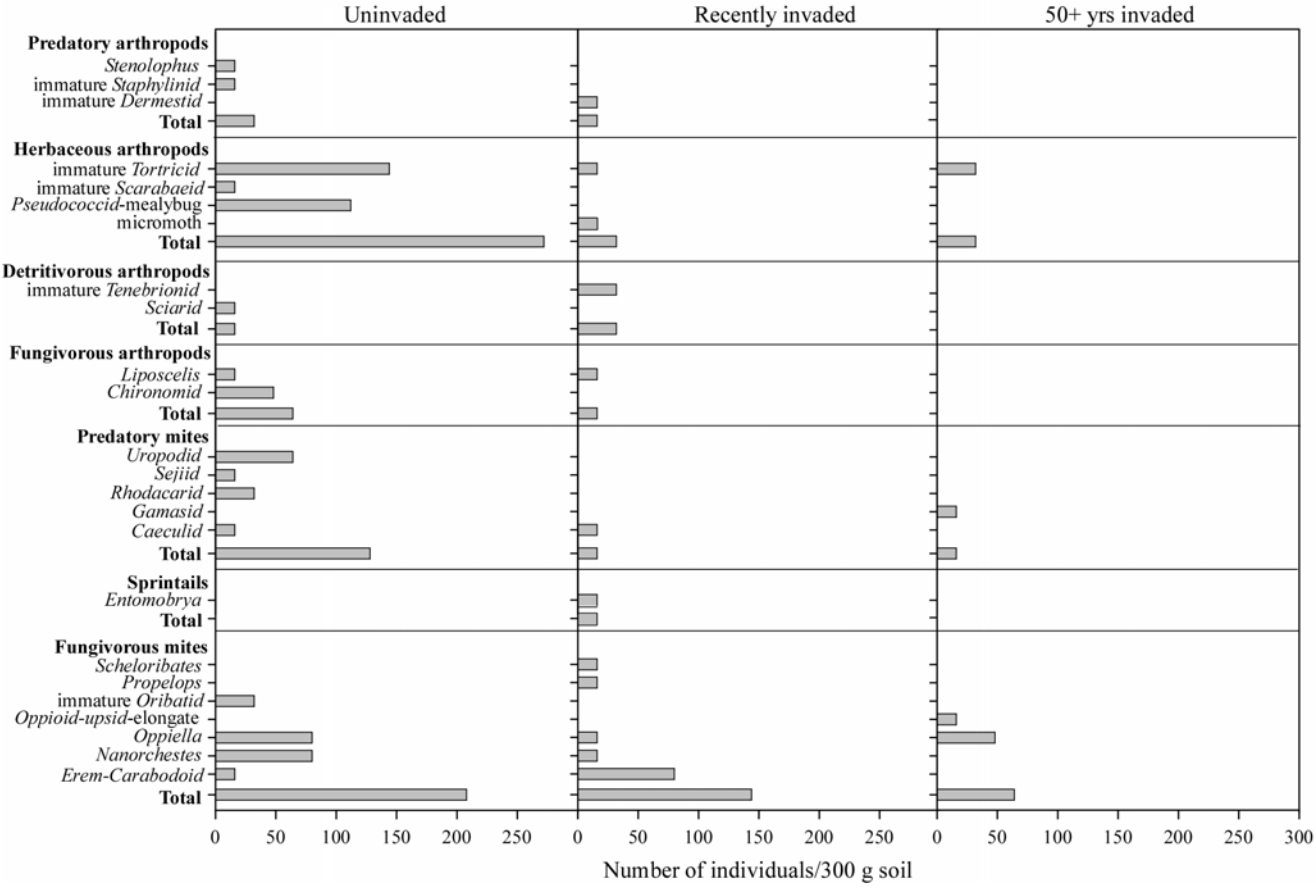


Figure 3. Numbers of species and individuals of microarthropods in soils at the uninvaded, recently invaded, and 50+ year invaded sites. Notice there are 16 species at the uninvaded site, 12 species at the recently invaded site, and only four species at the 50+ year invaded site.

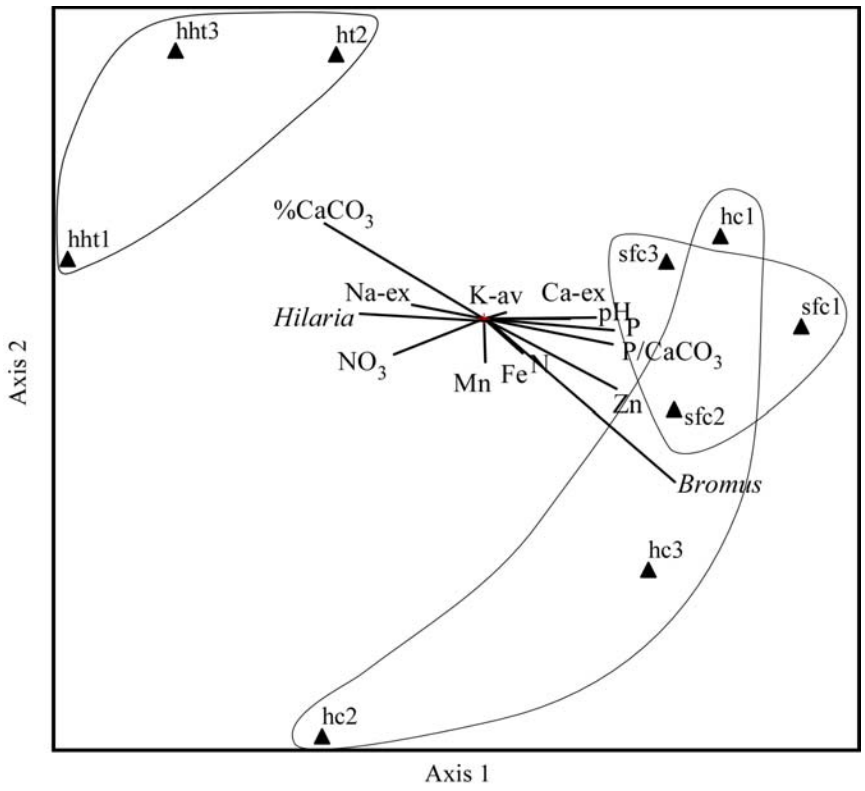


Figure 4. Ordination of soil food webs at the uninvaded, recently invaded, and 50+ year invaded site. Notice that the two invaded sites clump together and are very distinct from the uninvaded site. The invaded sites show higher K, N, zinc, and available P than the uninvaded site.

Year	Site	Mean	Std. Err.		*P*
Wet year	Uninvaded	12.0	± 1.0	a	0.004
	Recently Invaded	10.7	± 1.5	a	
	50+ yrs invaded	3.7	± 0.9	b	
Average year	Uninvaded	17.0	± 0.0	a	<0.0001
	Recently Invaded	12.0	± 0.6	b	
	50+ yrs invaded	2.7	± 0.9	c	
Dry Year	Uninvaded	6.7	± 0.9	a	0.06
	Recently Invaded	3.7	± 1.3	b	
	50+ yrs invaded	2.3	± 0.9	c	

Table 5. Plant species richness in a dry, average, and wet year at the uninvaded, recently invaded, and 50+ year invaded sites. Note that in the dry year, differences were statistically significant at P = 0.06.

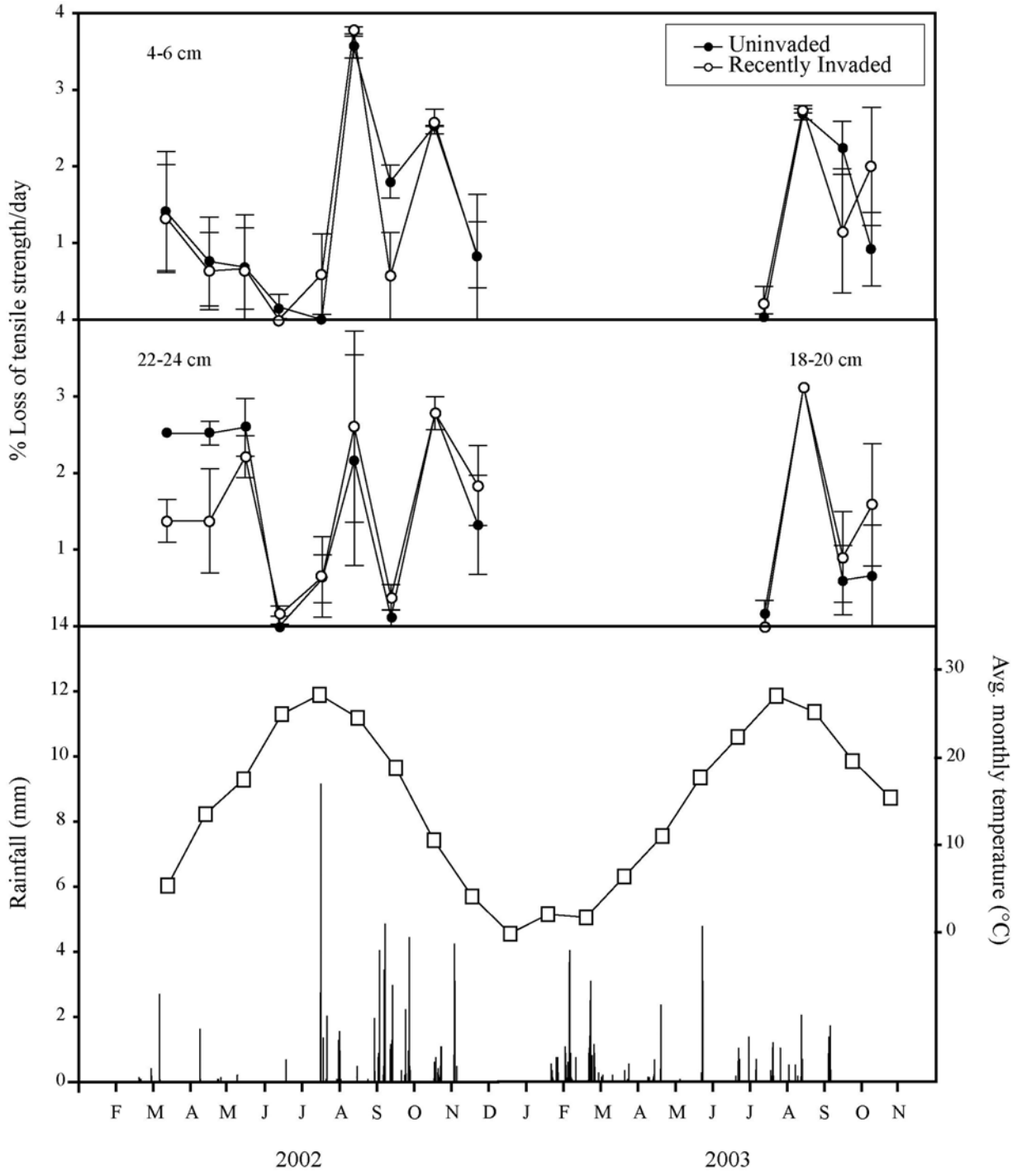


Figure 5. Decomposition rates at different times of year, precipitation, and temperature. Not that maximum decomposition rates occur when air temperatures are highest (which also correlates with plant sensecence), not when rainfall is greatest. In addition, there is no difference in rates with and without *Bromus*.

Soil chemistry: Because only one soil sample was analyzed for each of the three soils at the time of planting, statistical analysis could not be done on soil chemistry (Table 6). However, we have repeatedly measured soil chemistry at these sites over the past 7 years, and have found low variability (5-10 % of the mean for each element) within and among years. With this low variability in mind, there were several nutrient similarities and differences apparent in the soils at the time of planting that merit discussion, especially in light of the pattern of *Hilaria* biomass when grown in these soils. As was true for *Hilaria* biomass, the soils at the uninvaded and 50+ year site were very similar to each other and both of them were very different from the recently invaded site soils. Soils from the recently invaded site had higher levels of silt, organic matter, micronutrients, and available K, N, and P/$CaCO_3$ ratios (indicating higher P availability).

The soil chemistry elements most highly correlated with the NMS spatial ordination were mostly the same soil elements that appeared to differentiate the recently invaded site from the other uninvaded and 50+ year site in Table 6. Axis 1 (which separated the uninvaded from the two invaded sites) was correlated with zinc (R = 0.66), CaCO3 and P/$CaCO_3$ (R = 0.59), NO_3 (R = -0.56), Na (R = -0.44) and K (R = 0.24). Similar nutrients were correlated with axis 2 (which separated the uninvaded and recently invaded sites and helped separate the recently invaded and 50+ year sites to some degree): $CaCO_3$ (R = 0.51), zinc (R= 0.44), manganese (R = -0.35), iron (R = -0.31), P/$CaCO_3$ (R = -0.27), and total N (R =-0.25)(Figure 6).

Combined, the above data indicate that although the composition, richness, and abundance of bacteria, fungi, protozoa, nematodes, and microarthropods were very different among the sites among years, these differences did not explain the observed *Hilaria* growth patterns. Soil nutrient levels, on the other hand, appear to clearly explain the *Hilaria* results. Quite simply, plant biomass was greatest in the soil which had the highest levels of available N, P, and micronutrients. This is not surprising, as many studies have found the presence of invasives in general, and *Bromus* in particular, correlated with soil fertility (e.g., Huenneke et al. 1990; Muller and Garnier 1990; Burke and Grime 1996; Brooks et al. 1998; Hobbs et al. 1988; Stohlgren et al. 1998, 1999, 2001, Stohlgren 2002, Stohlgren and Chong 2002).

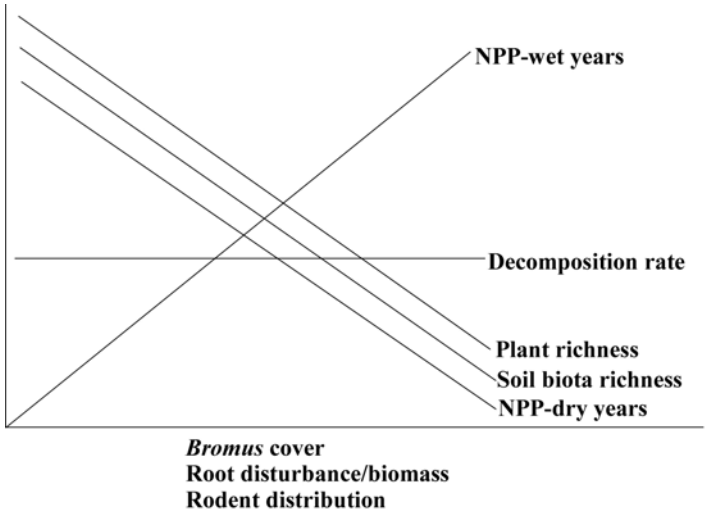


Figure 6. A conceptual model of the response of soil and plant species richness, net primary productivity, and decomposition rates to *Bromus* invasion and disturbance at these study sites. This response does not support the intermediate disturbance hypothesis.

	Univaded	Recently invaded	50+ yrs invaded
P, ppm	6.7	7.3	8.2
K available, ppm	195	186	291
% OM	0.3	**0.9**	0.5
pH	8.3	8.2	8.2
EC	0.5	**0.8**	0.7
% Sand	69	55	65
% Silt	16.5	**30.5**	18.5
% Clay	14.2	14.2	16.2
CEC	9.4	11.1	13.0
Zn, ppm	0.2	**0.6**	0.3
Fe, ppm	2.1	2.1	1.7
Mn, ppm	5.9	5.2	5.9
Cu, ppm	0.5	**1.2**	0.5
Ca exchangeable, ppm	3404	2612	3268
Mg exchangeable, ppm	119	200	158
K exchangeable, ppm	275	**517**	437
Na exchangeable, ppm	69	59	59
N, ppm	352	**484**	344
Min. NH_4^+-N, ppm	0.3	0.7	0.3
NH_4^+-N, ppm	10.2	8.7	6.1
NO_3^--N	10.8	**14.8**	9.7
% $CaCO_3$	5.3	2.5	4.5
P/$CaCO_3$	1.3	**3.0**	1.8

Table 6. Soil chemistry at the uninvaded, recently invaded, and 50+ year invaded sites. The numbers in bold are those discussed in the text. Although N=1 for these samples, our repeated measures at these sites indicate that these values are consistently elevated at the recently invaded site.

We do not mean to imply that the presence or absence of *Bromus* created the differences seen in soil chemistry among the three sites, as we did not measure these soils before invasion. Instead, we suggest that *Hilaria* was responding to soil nutrient differences that existed before the *Bromus* invasion and that the current differences in soil chemistry were more important in determining the *Hilaria* response when grown in these soils than the current structure of the soil food webs. This argument is supported by other data that suggests dominance by *Bromus* leads to soil N reduction in the long term (Evans et al. 2001). Soil and plant isotopic N are also highest at the 50+ year site, intermediate at the recently invaded site, and lowest at the uninvaded sites, further supporting the idea that *Bromus*-invaded sites lose N over time (Evans and Belnap, unpub). However, Svejcar and Sheley (2001) found *Bromus* had few consistent effects on soil N or N mineralization. We found that the 50+ year site and the uninvaded site had similar total soil N, suggesting that antecedent conditions were a stronger determinant of current soil nutrient levels than current invasion status. Phosphorus availability appears to increase with *Bromus* invasion in the short term (Sanford et al. in prep). However, as with N, the uninvaded and 50+ year site had very similar levels of P, again suggesting that site differences were present before the invasion and that the presence of *Bromus* has yet to overcome this initial difference.

We also need to address the question as to why *Hilaria* no longer grows at the 50+ year site. The soils will obviously support *Hilaria* growth, and it grows near the 50+ year sites. We believe the most likely explanation for the lack of *Hilaria* is that heavy grazing, combined with the invasion of *Bromus*, extirpated this species from these areas. *Hilaria* is a rhizomatous species that extends itself mostly by tillers and seldom reproduces by seed in this region, even under favorable establishment conditions (Belnap, per. obs.). It is likely that this very small seeded species has a difficult time competing with the fall-established *Bromus* plants, even if seeds reach these areas.

Synthesis: Despite the appearance that soil chemistry alone can explain our experimental results, we believe that relying on soil nutrient levels alone to explain differences in plant performance is overly simplistic, as many studies have shown soil nutrient availability is clearly tied to the composition, structure, and activity of soil food web organisms over time (Wardle 2002). There is a substantial literature on the positive relationship between the type and abundance of soil biota, especially soil fauna, and plant performance factors such as NPP, growth rates, leaf nitrogen contents (e.g., Ingham et al. 1985, Bonkowski et al. 2000, Kuikman and van Veen 1989). However, there are also studies that show no effect (Setälä et al. 1996, Laakso and Setälä 1999).Unfortunately, most studies directly examining the links between soil food webs and nutrient availability and/or plant performance have been done in laboratories under necessarily simplified conditions, often making it difficult to apply specific results to far more complex field situations. It is also difficult to know where a given soil lies at a given point in time in the feedback loop that occurs between soil nutrients and soil biota.

One would speculate that alterations in soil food web composition and abundance would result in changes in soil nutrients over time. However, 50 years is a long time and in this study, soil nutrients were still not altered sufficiently to affect *Hilaria* performance. These leaves several possible explanations of our data:

1. Alteration of soil biota may not affect plant performance until soil fertility drops below a threshold (unless a plant pathogen is introduced). This would imply that low fertility sites or plants with high nutrient demand will show impacts of changes in soil food webs before more fertile sites or those with less demanding plants, assuming the change in soil food webs lead to fertility loss. Alternatively, alterations in soil food webs may lead to greater fertility;

2. Large changes in soil food web organism abundance and species richness do not matter, as soil biota are generally sufficiently abundant and redundant in function to maintain soil fertility, at least for 50 years; and/or

3. There are key soil fauna (as found by Alphei et al. 1996, Ingham et al. 1985, Bonkowski et al. 2000) that determine plant response that were not measured (e.g., individual species of protozoa) or not adequately recognized in the analysis as drivers of *Hilaria* performance.

All the soils we used were already lower in N relative to soils in more mesic areas (Driscoll et al. 1999, Hobbs and Schimel 1984, Ellis and Graley 1983), as are most desert soils (West and Skujins, 1978). Yet, despite altered and depauperate soil food webs at the 50+ year site, these soils were still sufficiently fertile to support both *Bromus* (in the field) and *Hilaria* (in the greenhouse) In addition, *Bromus* is an annual plant and thus would be considered a plant with a high nutrient demand, yet it grows successfully at sites invaded for 5 and 50+ years. Therefore, our data would suggest that one or several of the following are true: 1) the threshold for N is very low for both *Hilaria* and *Bromus* and thus even a depauperate fauna can still provide the needed N; 2) N loss via the presence of *Bromus* is very low; 3) even these low N soils can support plants for some time before additional N is needed for normal plant growth and/or 4) the soil food webs present at all our sites were sufficient to keep providing the N needed by these plants, despite a large decline in abundance and species richness. This may be due to the presence of key species that keep nutrients flowing to plants. Although we did measure the major soil food web groups by genera or species (except protozoa), it would be easy to miss a key species without focusing the analysis on the species and/or doing addition or removal experiments.

The bigger picture

The findings of this study, combined with results from a previous study at some of the same sites, also illuminate several currently debated aspects of invasion and biodiversity theory:

Invasions occur where native plant and soil species richness is highest and where soil resources are greatest.

Elton (1958) long ago suggested that areas with low species diversity/richness should be more vulnerable to invasion than areas with higher species diversity/richness. There has been a great deal of recent debate of this topic (Tilman 1999, Stohlgren et al. 2003). Our data support the idea that the rich do, indeed, get richer (*sensu* Stohlgren): at our study site, *Bromus*-invaded areas with higher soil nutrients, plant species richness, and plant biomass (*Hilaria*-dominated sites) as opposed to immediately adjacent communities with lower nutrients, plant species richness, and plant biomass (dominated by *Stipa*)(Kleiner and Harper 1977, Belnap in prep). The *Hilaria*-dominated sites also had higher species richness and abundance of soil microarthropods (other soil biota were not analyzed for species richness) compared to *Stipa*-dominated communities (Belnap and Phillips 2001). During the past six years, *Bromus* has continued to creep into uninvaded, nutrient and species-rich *Hilaria*-dominated communities while avoiding uninvaded, nutrient and species-poorer *Stipa*-dominated communities. Clearly, in this instance, resistance to invasion was not greater in communities with a higher level of plant or soil species richness or abundance. Other studies support our findings that invasion occurs where soil resources are higher (Huston 1994, Wiser et al. 1998, Stohlgren et al. 1999, Davies et al. 2000).

Richness begats richness and stability: 1) greater richness in plant species results in greater richness of soil biota, 2) higher levels of soil resources results in higher soil biotic richness, 3) greater soil biotic richness results in greater soil process rates, and 4) greater richness results in greater stability.

1. Greater plant species richness results in greater soil biota richness. Plants influence many of the same factors that affect species richness of soil organisms, including soil carbon, temperature, moisture, and resource heterogeneity. Because individual plant species have very different influences on soil resources, it has been hypothesized that a greater richness of plants will result in greater heterogeneity of soil resources, and thus, greater richness of soil organisms and accelerated soil process rates. The study reported on here supports this hypothesis: the sites with the greatest plant richness (univaded *Hilaria*) supported a greater richness of nematode genera and fungal and microarthropod species (the only groups analyzed for richness), while the sites that had the intermediate plant species richness (the recently invaded site) supported an intermediate richness of nematodes and microarthropod richness. The sites with the least plant species richness (the 50+ year site) had the lowest species richness of microarthropods, fungi, and nematodes.

Other studies support this hypothesis as well. Anderson (1978) showed that cryptostigmatid mite richness increased with increased habitat diversity. Other studies have shown increasing the types of plant litter increased gastropod and mite richness and decomposition rates (Barker and Mayhill 1999, Hansen and Coleman 1998, Kaneko and Salamanca 1999, Hansen 2000). Hooper and Vitousek (1997, 1998) showed that when the number of plant functional groups was increased from one to two groups, there was an increase in microbial biomass, N immobilization, and resource use by plants.

However, other studies have not shown a positive relationship between plant species richness and soil biotic richness. At our site, a previous study showed microarthropod richness was far higher in the uninvaded *Stipa*-dominated patches with the lower plant diversity than in the uninvaded *Hilaria* -dominated site with greater plant species richness (Belnap and Phillips 2001). In the Hooper and Vitousek studies (1997, 1998), they saw no effect when the number of plant functional groups was increased above two functional groups, indicating that the positive effects of plant species richness on belowground biota is unlikely to be operative in many “real” world situations, as most plant communities support more than two functional groups. Aberdeen (1956) found no effect on fungal biomass when plant richness was increased. Wardle and Nicholson (1996) showed plant richness had a mixed effect on soil microbial respiration and biomass, as well as decomposition rates. Hector (2000b) found litter mass loss rates were only weakly related to the number of plant litter types. Effects of plant litter richness on soil biotic richness was also mixed and appeared dependent on the species of soil organisms present and the type of plant litter used (e.g., Blair et al. 1990, Wardle et al. 1997, Chapman et al. 1988).

The large variability in the responses above suggests that the relationship between plant and soil biota richness is predicated on the specific plants involved, and that no general relationship with richness exists. This finding has been supported by multiple studies. Monospecific plant stands can support greater mite diversity than stands with greater plant richness and specific tree species can support higher mite diversity than other species (Badejo and Tian 1999. Hansen 1999). David et al. (1999) showed that shrub sites had twice the macrofaunal species than forest sites. Eom et al. (2000) showed that arbuscular mycorrhizal fungal richness differed on specific grass species. There have also been studies showing that as species are added to the community, there are changes in microbes (Skujins and Klubek 1982,

Frankland 1998), nematodes (Wasilewska 1994), and arthropods (Paquin and Coderre 1997). At our site, the addition of a single species (*Bromus tectorum*) to two adjacent grass communities (*Stipa* and *Hilaria*-dominated) had a large effect on soil biota, but the effect was vastly different in the two communities: *Bromus* enhanced soil biotic richness in the *Hilaria* community while depressing it in the *Stipa* community (Belnap and Phillips 2001). Gremmen et al. (1998) also saw that when *Agrostis stolonifera* entered into a shrub community on Marion Island, numbers of some soil groups were enhanced, whereas abundance in other groups were depressed.

2) Higher levels of soil resources results in higher soil biotic richness: There have been multiple studies showing a positive correlation between higher levels of soil resources (e.g., carbon, nutrients) and soil biotic richness. These include Wright and Coleman (1993) for nematodes, Schaefer and Schauermann (1990) for many faunal groups, and Paoletti (1988) for chilopods and isopods. Wardle (2002) reported seven studies that all showed decomposer richness increasing with soil resources. However, in this study, we did not see such a relationship. Nematode generic and microarthropod species richness (highest in the uninvaded sites) was not associated with levels of soil nutrients or root biomass (highest in the recently invaded sites) but instead were correlated with plant diversity and lack of soil surface disturbance (both highest in the uninvaded site).

3) Greater soil biotic richness results in greater stability of communities and processes, as well as higher process rates: The idea that greater species richness confers stability upon communities has been presented by multiple authors in many forms (e.g., Grime 1998, Walker et al. 1999). The underlying concepts of most arguments has been that greater species richness is accompanied by a greater probability that a species necessary to carry out a specific function will "match" future conditions (that may or may not be predictable). A corollary of this is that species that currently may appear "redundant" might be critical under these changed conditions (Andren et al. 1995). However, it has also been argued that maintaining function in the face of perturbation only requires the right combination of species to be present after the perturbation and that richness *per se* does not assure these particular species will be present (Wardle 2002). Therefore, soil biota may are affected by the removal (e.g., natives) or addition (e.g., invasives) of specific plant species with specific functional traits, but not by a reduction in richness *per se* (Wardle et al. 1999). This has been demonstrated across a wide variety of habitats (Cavigelli and Robertson 2000, Gulledge and Schimel 1998, Saggar et al. (1999).

Our data do not support the idea that greater species richness results in greater community or process stability. At our sites, soil biotic richness clearly declines with invasion by *Bromus* (this study, Belnap and Phillips 2001). Yet despite large, observed reduction in the number of species and individuals, the system appears as "functional" after the invasion as it was before the invasion, if function is defined in terms of decomposition rates and the ability of the system to deliver soil nutrients needed for growth of the original dominant plant species. This suggests there is either considerable functional redundancy in the soil fauna at our study sites or that the species critical to decomposition and nutrient cycles remain despite *Bromus* invasion. In any case, our data suggest that unless specific species involved in specific processes are reduced or eliminated, the ecosystem effects of disturbance can be minimal for an extended period of time. This same conclusion has been suggested by multiple authors (Andren et al. 1995, Lawton et al. 1996, Ettema et al. 1998, Mikola and Setala 1998).

There is some evidence that changing soil food webs can alter process rates (Degens 1998, Griffiths et al. 2000). Again, however, Wardle (2002) maintains that soil biotic richness or diversity in natural systems are not likely to be reduced to the point that the decomposer

community as a whole is affected. Wardle's position is supported by several studies, including that of Schwartz et al. (2000), who found that although increasing species richness reduced the variance of specific process measures, this reduction saturated at a very low number of species. As was the case with our study, other studies have shown that reduction in soil food web diversity does not affect decomposition rates (Andren et al. 1995, Lawton et al. 1996, Ettema et al. 1998).

Intermediate levels of disturbance result in greater resource heterogeneity which results in diversity/richness and site productivity.

The intermediate disturbance hypothesis has been successfully used to explain the structure and function of many ecosystems (e.g., Grime 1973, Connell 1978, Huston 1979). This hypothesis argues that species diversity/richness should be highest at intermediate levels of disturbance, as intermediate levels of disturbance result in a greater heterogeneity of resources and habitats than when disturbance is severe or never occurs. Regardless of how disturbance is defined, our results do not support this hypothesis (Figure 6). If the invasion of a plant species is defined as a disturbance, our recently invaded site would represent an intermediate level of disturbance, as native plants have not yet been extirpated (as has occurred in our 50+ year site). However, soil biotic richness was greatest at uninvaded site, not the recently invaded site. If disturbance is defined as the disruption of the soil surface by burrowing rodents, this hypothesis again does not explain our results. As *Bromus* cover and seed production increases, so does the burrowing rodent population and attendant churning of the soil surface (Belnap, pers. obs). Therefore, the uninvaded sites have the least disturbed soil surface, the 50+ sites have the most disturbed soil surfaces, and the recently invaded site represent the intermediate level of disturbance. However, the recently invaded site has an intermediate levels of soil biotic (fungi, nematodes, microarthropods) and vascular plant species richness rather than the highest levels predicted by this hypothesis. Plant productivity at these sites also does not follow predictions made by the intermediate disturbance hypothesis, as the greatest disturbance level (as defined by invasion or soil disturbance) is associated with the greatest plant productivity in wet years and the lowest productivity in dry years, as *Bromus* productivity is highly responsive to current precipitation patterns. Given the wide swings in *Bromus* productivity at these sites, community stability (as defined by predictable biomass and community composition) was also lowest in the 50+ year site and highest at the uninvaded site.

Similar to our results, Yeates and Bird (1994) and Freckman and Ettema (1993) also found nematode diversity increased as disturbance decreased. Huston (1994) and Wootton (1994) suggest that patterns in diversity or richness of higher trophic level species (e.g., nematodes, microarthropods) may be less likely explained by the intermediate disturbance hypothesis than plant diversity, again similar to the results reported for the present study. Also consistent with our findings, Wardle (2002) suggests that soil biotic diversity does not follow the intermediate disturbance, but instead generally shows a monotonically declining response to disturbance. He speculates that this is probably a result of low competition among soil groups relative to other factors that regulate soil biota.

Ecological Legacies of Invasion

We believe the concept of ecological legacies has a central role to play in invasion theory, and, in turn, invasion theory can expand the current applicability of ecological legacies. Ecological legacy theory postulates that post-LID ecosystem trajectories depend on conditions

before and after the disturbance, as well as the type and timing of the disturbance. Similarly, a large-scale invasion by a non-native species can clearly constitute a large, infrequent, and "unplanned" disturbance. (As with LIDs, we are restricting this discussion to invaders that occur on a landscape scale, such as *Bromus*.) And as with other disturbances, the ecosystem trajectory after invasion will be a result of antecedent conditions (e.g., soils, climate, other species present), the timing (e.g., season, phenological stage) and type (i.e. the invading species) of the disturbance, and conditions following the disturbance (e.g., soils, climate, other species present). Broadening the concept of ecological legacies to include invasions will require characterizing different invasion events and defining some broad categories of ecosystem effects associated with invaders, as has been done for other disturbance types (see Table 1 and 2 in Foster et al. 1998). Whereas their matrix is focused on landscape-level abiotic factors, we suggest that the inclusion of invasions will require also focusing on the catena-scale and both biotic and abiotic factors. Foster et al. (1998) distinguish among the following types of LIDs: volcanic eruptions, tornados, forest fires, hurricanes, and riverine floods. As the LID categories need to be kept to a minimum, we propose there is at least one fundamental distinction to be made among invaders: those that have the potential to alter their surroundings or native species populations such that the potential of the habitat to support the previous-occurring species is lost even though the invader is removed (e.g., *Tamarix*, which can salinize the soil beyond the tolerance of native *Salix* and *Populus*; *Halogeton*, which increases soil salinity and may introduce pathogens) and those that have a large impact while present but if removed, have not altered the habitat such that previously-occurring natives cannot re-establish, assuming propagules are still present (*Bromus*). Foster et al. also suggest categories for characterizing the effects of a LID such as the type and duration of the event, return intervals, etc. We would suggest adding the alteration of native floral or faunal composition, alteration of available soil nutrients or water; alteration of trophic interactions. In order to be the most effect, it would also help to differentiate between short and long-term effects.

Conclusion and Future Research Directions

Our goal was to evaluate whether the short- or long-term dominance of a site by the invasive annual grass *Bromus* leaves behind a legacy of altered soil biota and chemistry such that native grass growth (*Hilaria*) is suppressed. Our results indicate that *Hilaria* growth responded to soil chemistry antecedent to the invasion, not to changes in soil food web composition or abundance or chemistry following invasion. These findings should be encouraging to land managers, as it appears likely that no restoration of soil food web populations are required for native plants to succeed in *Hilaria* soils, unless plant pathogens have been introduced. Future research efforts are needed to establish if these same patterns are true for other soil types, climatic regimes, and other native and exotic plant species. We also need further exploration of the mechanisms linking soil food webs to soil nutrient availability.

Long term dominance by *Bromus* is likely responsible for the low abundance and richness of the soil biota we saw at these sites. However, despite this reduction, plant-available nutrients are still present in sufficient quantity to support the once-dominant native plant species. We believe this supports the argument that species richness *per se* does not determine ecosystem process rates, but instead that the main biotic controls of ecosystem function are likely to be the interaction among the key traits of a few critical species, other species in the community, and the abiotic environment. To assist in restoration of disturbed lands, it would be valuable to know the identity of the critical species and how they affect other species and ecosystem function.

We also suggest that the theory of ecological legacies could benefit by the inclusion of landscape-level invasion of exotic species. This would require broadening the definition of LIDs, while more precisely defining the characteristics of an invasion, including the ecological consequences of that invasion. This framework could then be used to structure inquiry into predicting the effects of landscape-level plant invasions.

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Final Conclusions

During this project, we have learned a great deal about the characteristics of exotic annual grasses in general, and specifically *Bromus tectorum*. We have determined that soil chemistry plays a major role in determining whether or not a site will be invaded, and that other site characteristics (e.g., microhabitat, herbivory) are not as important. We determined that the availability of phosphorus and potassium are the most important elements to consider in desert environments. Because soil chemistry is mappable, resistance to invasion is also mappable. Factors operative at a local scale are applicable at a regional scale unless environmental conditions are very different (e.g., very low to high elevations). However, controls on annual grass differ among regions. This correlative study needs to be followed up with experimental manipulations to determine the mechanisms behind the observed patterns.

Based on the influence of soil chemistry on annual grass invasion, we also investigated soil amendments that can successfully suppress *Bromus*, yet have little effect on native plants. We found *Bromus* to be very salt-sensitive, whereas native grasses are salt-tolerant and thus, *Bromus* could be suppressed with the simple addition of NaCl (table salt). However, there is evidence that the effect of the tested amendments in the field change with precipitation regimes and over time and amendments that suppressed *Bromus* in one year can actually stimulate it the next year. Therefore, before any of these amendments are used, long-term experiments are needed.

The presence of native plants stimulates *Bromus* growth. We need to understand the mechanisms behind this observation, as this will impact any restoration effort.

Once *Bromus* invades, it has differential effects on the native communities, depending on what species are present prior to the invasion. In the absence of grazing and fire, *Bromus* did affect vascular plant communities. Therefore, restoration of invaded grasslands appears to be a reachable management goal, but may require restriction of other disturbances. However, *Bromus* did accelerate the decline in cover of the dominant lichen *Collema*. Because *Collema* is the major source of nitrogen for this ecosystem, this is of great concern. Therefore, restoration efforts should include inoculation of this lichen. Ways to enhance restoration of this lichen need to be explored.

Bromus was also shown to alter soil P. However, changes in soil P appear to be seasonal (winter) and only during wet years. Changes in N availability appeared minor in the heavily-invaded *Hilaria* communities. Therefore, these changes are unlikely to favor *Bromus* over natives during restoration efforts. However, increased N cycling rates will likely decrease soil N over long time periods (>100 years). Although *Bromus* alters nutrients only slightly, it dramatically alters both the abundance and species composition of soil food webs. However, site alterations by *Bromus* do not affect the ability of these soils to support growth of the native grass *Hilaria* that once dominated these soils. Therefore, managers likely do not need to manipulate soil food webs or soil chemistry to successfully restore invaded areas.